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Miocene plants from Colombia, South America

EDWARD W. BERRY

(WITH PLATES 2 AND 3 AND TWO TEXT-FIGURES)

The plants described in the following notes have been turned over to me from time to time during the last few years by the Tropical Oil Company. They come from three localities on the De Mares concession, which is located in the Magdalena Valley, Department of Santander, Colombia, about 350 miles south of the Caribbean coast.

Relatively little is known regarding the Tertiary floras of Colombia. With the exception of two species of fossil fruits described recently without locality by E. M. Reid,[1] the previous contributions were enumerated by me[2] in 1929 and need not be repeated in the present connection.

The material is limited in amount and rather poorly preserved and it has been possible to make more or less satisfactory identification of only 17 different forms. These represent 16 genera in 13 families and 11 orders.

All belong to the dicotyledonous angiosperms except 2 species representing 2 families and 2 orders of Monocotyledonae. They are wet tropical forms and obviously do not present any sort of picture of the flora which must have existed in the region at the time they were living. Many families which inhabit the country at the present time and which were undoubtedly present during the latter half of the Tertiary, for example, the Leguminosae, are not represented.

Nor can anything be said about the ecology except that certain of the fossils represent coastal forms, such as the *Avicennia*, and others occur in Tertiary floras of known coastal habit, so that there is some slight evidence that the sea margin was not far distant at the time the plants were preserved. Four species are new, and several others which are too poorly preserved for specific description, appear to represent new forms. Nine species have an outside distribution and three additional are represented in other areas by closely related forms. These facts and the local distribution are shown in the accompanying table.

AGE OF THE DEPOSITS

The fossil plants from the De Mares concession are much too few in number and too indefinite specifically to afford a basis for close correlation, and even if they were more abundant, well preserved and certainly determinable, the question of exact age would still be a problem, since most of the outside localities with which they might be compared are somewhat

[1] Reid, E. M. Rev. Géogr. Phys. & Géol. Dynamique, **6**, fasc. 3, 1933.

[2] Berry, E. W. Proc. U. S. Natl. Mus. **75**, art. 24: 1–12, pls. 1–5, 1929.

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uncertain in age due to differences of opinion among the students who have studied the various deposits.

One thing at least is certain, i.e., the three stations from which fossil plants have been collected on the concession are at least approximately of the same age, as is shown by the fact that the two species found at Station 19 N., 2 W. are present at both of the other stations, and one of these, *Mespilodaphne colombiana*, is a new species unknown at outside localities; and of the seven species named from Station 35 S., 25 W., all but two are present at one or the other of the other two stations.

	27 N., 2 E.	19 N., 2 W.	35 S., 25 W.	COLOMBIA: SANTA ANA	COLOMBIA: LEIVA	COLOMBIA: BUGA, CAUCA VALLEY	VENEZUELA: BETIJOQUE	VENEZUELA: LA VICTORIA	VENEZUELA: PALMAJERO	TRINDAD B.W.I.: SIPARIA	TRINDAD B.W.I.: FOREST SAND	LOJA, ECUADOR	COSTA RICA	TEHUANTEPEC, MEXICO	ZORRITOS FORMATION PERU	COLLAZO SHALES PUERTO RICO
Dioscorea sp.	x						o						o			
Palmophyllum sp.	x		x				o		o							
Ficus talamancana													x	x		
Ficus cf. betijoquensis	x						x									
Coussapoa sp.	x		x				o							o		
Anona cf. guppyi	x		x				x	x								
Tapirira lanceolata	x								x			x			x	
Rheedia miocenica			x							x						
Buettneria sp.	x			o												
Hernandia tongi	x							x								
Persea coriacea			x	x	x											
Mespilodaphne colombiana	x	x	x													
Eugenia comparabilis	x	x	x							x	x					x
Couroupita santanderensis																
Avicennia miocenica	x															
Posoqueria columbiana						x										
Phyllites sp.	x															

x = Identical.
o = Similar.

Another certainty is that the age is Miocene. There can be no doubt of this, but whether Lower, Middle, or Upper remains doubtful. As will be seen in the accompanying table of distribution one species, *Persea coriacea*, is known from beds which seem to be Upper Miocene, but about which no certainty can be expressed. Four come from beds elsewhere which are either Lower or Middle Miocene, three from beds which are Middle or Upper Miocene, and one from beds which are Lower to Upper Miocene. I have also shown in the table outside formations containing plant species most similar to De Mares species. Among these there are

three whose age is Lower or Middle Miocene and one from beds which are Middle or Upper Miocene.

Evaluating this distribution for what it appears to be worth it would seem to me that the De Mares plant bearing outcrops are probably of Middle Miocene age, but I would certainly not be dogmatic in that opinion.

In a preliminary report to the Tropical Oil Company on two specimens from Station 27 N., 2 E., dated July 25, 1930, I stated that although not certain they appeared to be of Upper Miocene age. The larger collections received after that date render the question of age more instead of less confusing. It is possible that the age may be Upper Miocene.

Order LILIALES
Family DIOSCOREACEAE
Genus DIOSCOREA Linné
Dioscorea sp.
Text-figure 1

Leaves of large size, presumably cordate, with entire margins, stout petiole and palmately 7 to 9 veined from the top of the petiole. Secondaries mostly transverse. The single specimen, preserved in a coarse matrix, is very vague away from and between the primary veins and it is not possible to frame a satisfactory diagnosis. In many ways it suggests comparisons with the somewhat smaller leaves from the Miocene of southern Costa Rica which were described as *Piperites cordatus*[3] and which also appear to be present at Betijoque, Venezuela, and in the Forest Sand of Trinidad, B. W. I. Probably none of these are specifically identical with one another. The genus has not before been found fossil, but the family is represented by the genus *Dioscorites* Saporta from the Upper Cretaceous to the Oligocene, and possibly by the genus *Majanthemophyllum* O. Weber with numerous species from the Mid-Cretaceous to the Lower Miocene. *Dioscorea* has over 200 existing species, cosmopolitan in warm climates and sometimes extending long distances into the Temperate zone.

Occurrence: 27 N., 2 E.

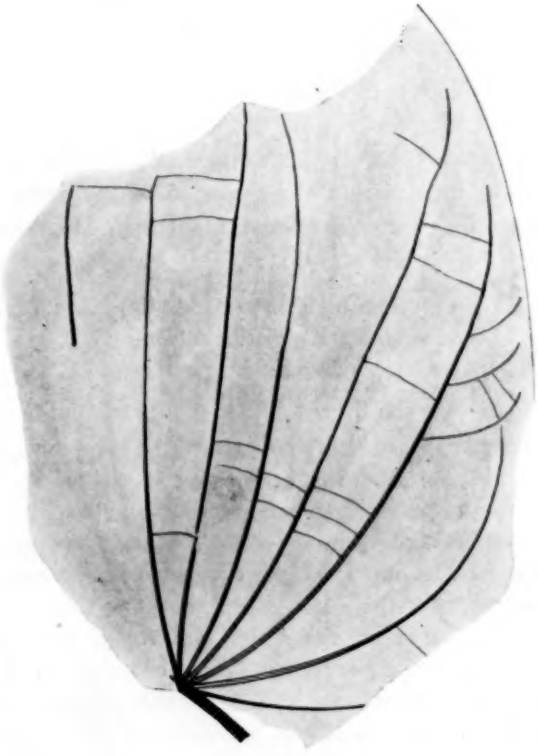
Order ARECALES
Family ARECACEAE
Genus PALMOPHYLLUM Conwentz
Palmophyllum sp.

Fragments of palm rays are referred to the genus *Palmophyllum* as a form genus. They may be the same as what was called *Sabalites* sp.[4] from Betijoque, State of Trujillo, Venezuela. They are too inconclusive to be of either geo-

[3] Berry, E. W. Proc. U. S. Natl. Mus. **59**: 171, pl. 22, fig. 1, 1921.
[4] Berry, E. W. Proc. U. S. Natl. Mus. **59**: 562, pl. 109, fig. 3, 1921.

logical or botanical interest beyond indicating the presence of palms in this fossil flora.

Occurrence: 27 N., 2 E. and 35 S., 25 W.



Text-figure 1

Dioscorea sp.

Order URTICALES
Family MORACEAE
Genus FICUS Linné
Ficus talamancana Berry
Plate 2, Figure 1

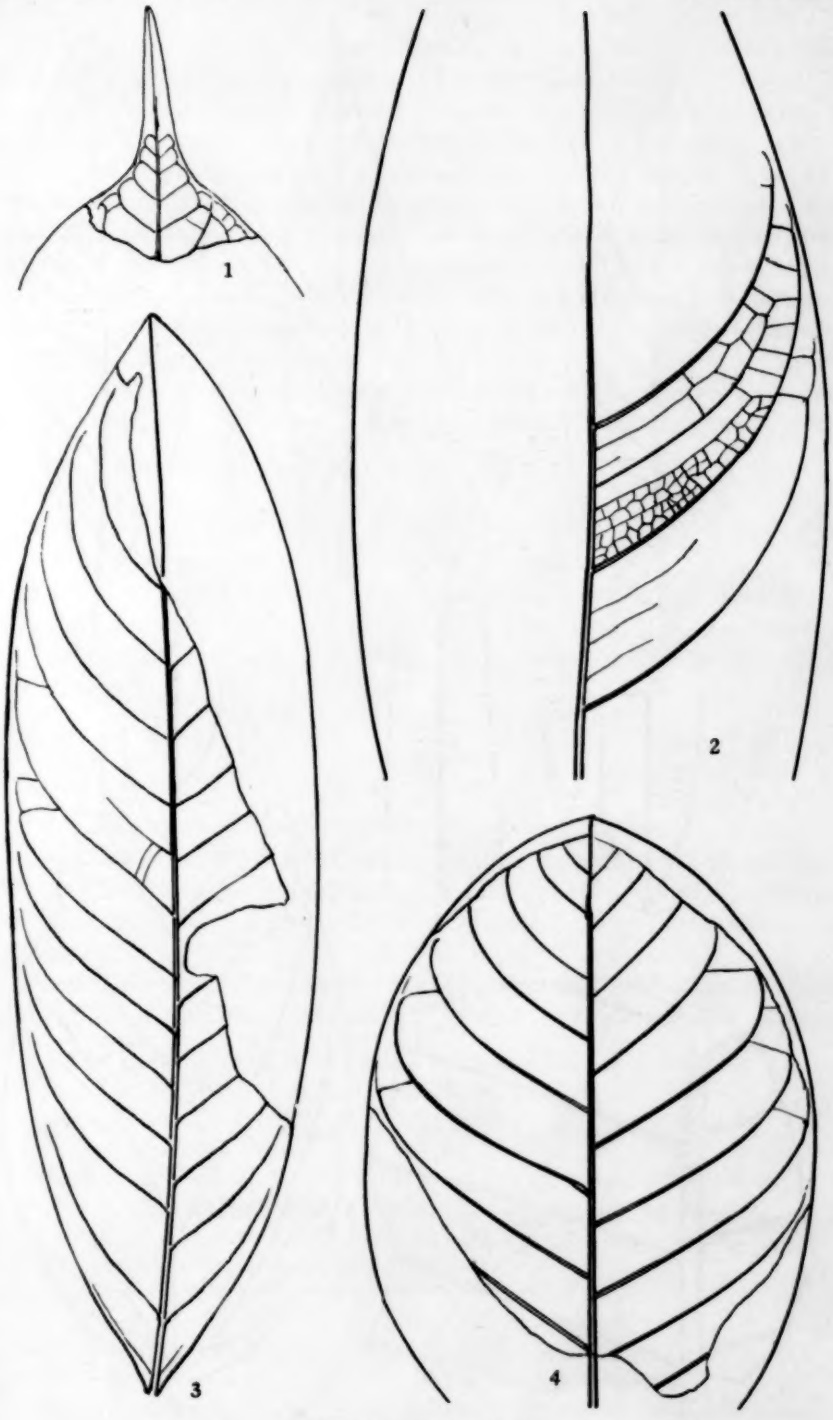
Ficus talamancana Berry, U. S. Natl. Mus. Proc. **59**: 172, pl. 23, 1921.

A single markedly apiculate tip of a *Ficus* leaf proves to be identical with

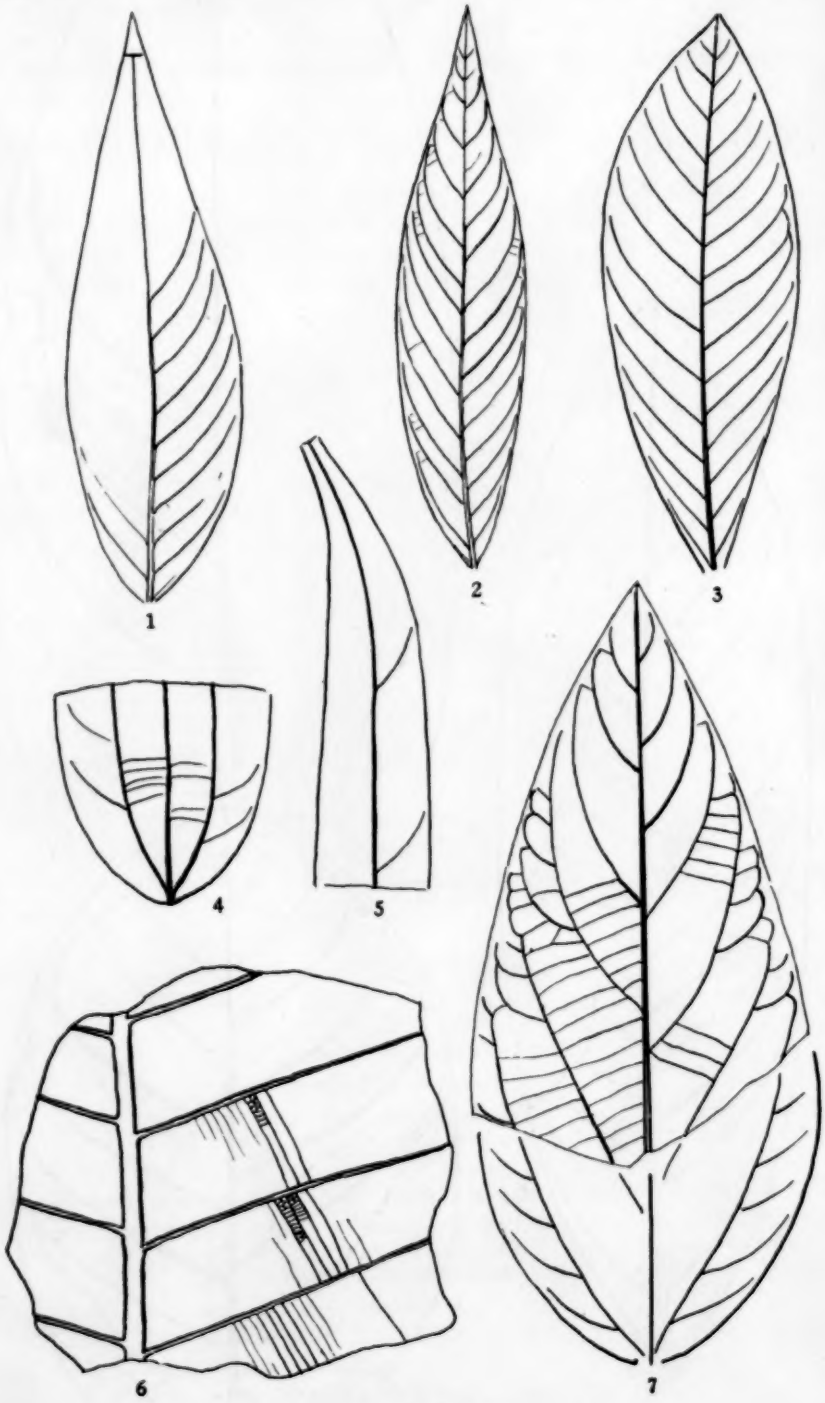
Explanation of plates

Plate 2

Fig. 1. Ficus talamancana Berry
Fig. 2. Persea coriacea Engelhardt
Fig. 3. Couroupita santanderensis Berry, n. sp.
Fig. 4. Posoqueria columbiana Engelhardt



BERRY: MIOCENE PLANTS



BERRY: MIOCENE PLANTS

a species from the Middle Miocene of southern Costa Rica, which was based upon material showing both surfaces of the whole leaf.

Leaves large, elliptical in general outline. Tip apiculate-acuminate, the acumen upwards of 3 centimeters in length. Base decurrent. Margins entire, full and evenly curved. Texture subcoriaceous. Length ranging from 14 to 16 centimeters. Maximum width ranging from 5.5 to 7 centimeters. Petiole stout. Midvein very stout, prominent on the under side of the leaf, relatively narrow on the upper side. Secondaries below the tip 8 or 9 subopposite to alternate pairs, diverging from the midvein at wide angles, 75 to 80 degrees, relatively straight and subparallel until they approach the margins where they are camptodrome. Tertiaries thin.

This handsome form may be matched by existing species in both hemispheres among the very numerous species of this cosmopolitan genus.

Occurrence: Station 35 S., 25 W.

Ficus cf. betijoquensis Berry
Text-figure 2, No. 2

A small but rather characteristic basal fragment of a leaf from Station 27 N., 2 E. probably represents this species, but in view of its incompleteness is not positively determined. The species was described[5] originally from Betijoque, Venezuela.

Genus Coussapoa Aublet
Coussapoa sp.
Plate 3, Figure 6

Small but characteristic fragments of leaves of this genus are present at two localities in the De Mares Concession. Since the features which permit the generic identification of fragments is the character of the tertiary venation, and since this is very similar in the different species, no specific determination is possible.

Species have been described in recent years from the Miocene or Pliocene of Mexico,[6] Colombia,[7] Venezuela,[8] Trinidad,[9] Ecuador[10] and Bolivia.[11]

[5] Berry, E. W. Proc. U. S. Natl. Mus. **59**: 566, pl. 108, fig. 5, 1921.

[6] Berry, E. W. Proc. U. S. Natl. Mus. **62**, art. 19, p. 6, pl. 2, 1923.

[7] ——— Idem. **75**, art. 24, p. 4, pls. 3, 4, 1929.

[8] ——— Idem. **59**: 563, fig. 2, pl. 108, figs. 1–4, 1921.

[9] Hollick, A. Bull. N. Y. Bot. Garden **12**: 296, pl. 6, fig. 1, 1924; Berry, E. W., Johns Hopkins University Studies in Geology No. 6, p. 86, pl. 1, fig. 4, 1925.

[10] Berry, E. W. Idem. No. 10, p. 99, pl. 3, fig. 9, 1929.

[11] ——— Idem. No. 4, p. 168, pls. 4, 5, 1922.

Plate 3

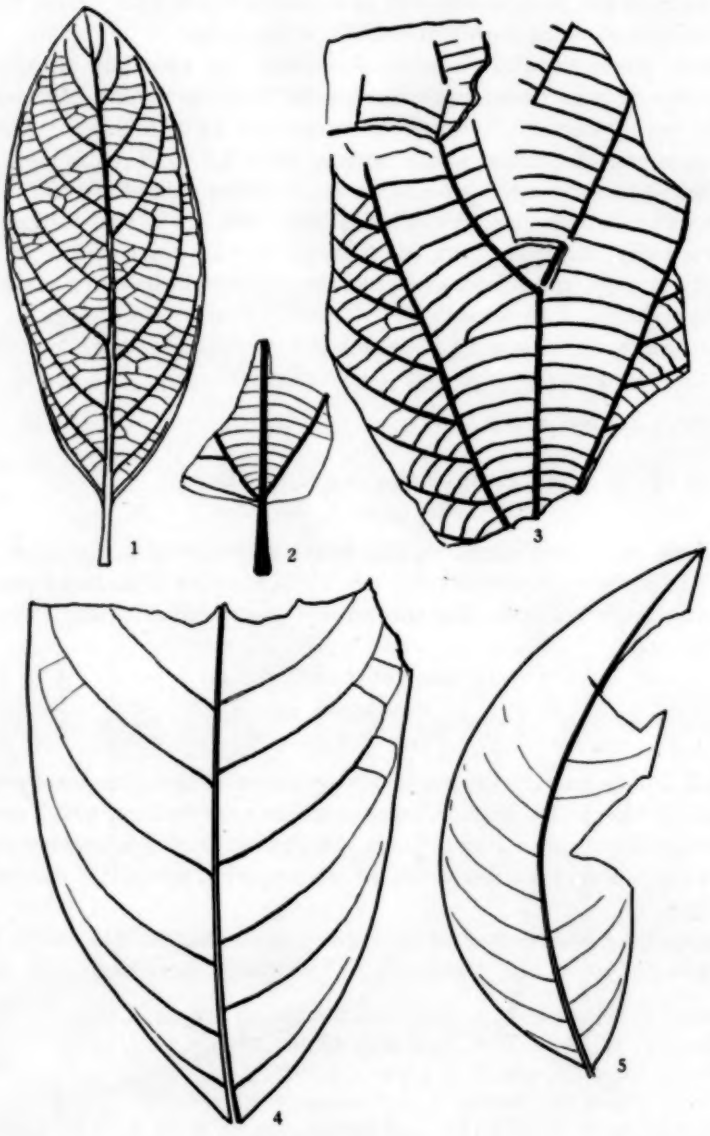
Figs. 1–3. Avicennia miocenica Berry, n. sp.

Fig. 4. Buettneria sp.

Fig. 5. Phyllites sp.

Fig. 6. Coussapoa sp.

Fig. 7. Hernandia Tongi Berry



Text-figure 2

No. 1. Mespilodaphne colombiana Berry, n. sp.
2. Ficus cf. betijoquensis Berry
3. Hernandia Tongi Berry
4. Anona cf. Guppyi Berry
5. Tapirira lanceolata Engelhardt

Among these the present fragments appear to be most like *Coussapoa villosoides* Berry from near Betijoque in the State of Trujillo, Venezuela, and Lower or Middle Miocene in age.

The genus contains about 15 existing species of shrubs and trees confined to the tropical rain forest from southern Mexico to the Bolivian Yungas and Brazil.

Occurrence: 27 N., 2 E. and 35 S., 25 W.

Order ANONALES
Family ANONACEAE
Genus ANONA Linné
Anona cf. Guppyi Berry
Text-figure 2, No. 4

A specimen showing about half of a leaf from Station 27 N., 2 E. is very close, if not identical, with *Anona Guppyi* described originally[12] from the Miocene of Betijoque, Venezuela. I believe it to be this species but in view of its incompleteness hesitate to so identify it. A fragment is also present at Station 35 S., 25 W.

Order SAPINDALES
Family ANACARDIACEAE
Genus TAPIRIRA Aublet
Tapirira lanceolata Engelhardt
Text-figure 2, No. 5

Tapirira lanceolata Engelhardt, Abh. Senck, naturf. Gesell. **19:** 15, pl. 9, fig. 4, 1895; Berry, Proc. U. S. Natl. Mus. **55:** 291, pl. 15, fig. 1, 1929.

This species was described by Engelhardt from the Interandean basin of Loja in southern Ecuador in deposits which are late Miocene or Pliocene in age, and what appears to be the same species occurs in the Lower Miocene Zorritos formation in northwestern Peru.

It belongs to a small genus of existing shrubs and trees with odd pinnate leaves, not otherwise known in the fossil state, confined to the South American tropics, and was compared by its describer with the existing *Tapirira guianensis* Aublet.

Occurrence: 27 N., 2 E.

Order PARIETALES
Family GUTTIFERAE
Genus RHEEDIA Linné
Rheedia miocenica Berry

Rheedia miocenica Berry, Johns Hopkins University Studies in Geology, No. 6, p. 109, pl. 5, fig. 3, 1925.

This species was described from the porcellanite of Siparia, Trinidad, B. W. I. A complete specimen occurs in the collection from 35 S., 25 W. The

[12] Berry, E. W. Proc. U. S. Natl. Mus. **59:** 567, figs. 1–4, 1921.

genus is distinguished with difficulty from the related genus *Calophyllum*. The existing species are arborescent and confined to the region between the Antilles, eastern Peru and Rio de Janeiro, Brazil. The only other fossil species known comes from the Pliocene of Bahia, Brazil.

Order MALVALES
Family STERCULIACEAE
Genus BUETTNERIA Linné
Buettneria sp.
Plate 3, Figure 4

This fragment from Station 27 N., 2 E. appears to represent the genus *Buettneria* but is too incomplete to be properly characterized. It is rather similar to a form from Santa Ana, Colombia, described by Engelhardt as *Buettneria cinnamonifolia*[13] and is also not unlike a form from Loja, Ecuador, which this author referred to the Lauraceous genus *Camphoromoea*.

The genus embraces about 50 existing species, the majority of which are found between the Antilles and northern Argentina. Fossil species are known from the Eocene onward.

Order LAURALES
Family HERNANDIACEAE
Genus HERNANDIA Linné
Hernandia Tongi Berry, n. sp.
Plate 3, Figure 7; Text-figure 2, No. 3

Leaves of medium to small size for this genus, ovate in outline, with a broadly rounded base and an acuminate tip. Margins entire. Texture subcoriaceous. Length ranging from 10.5 to 17 centimeters. Maximum width, at or below the middle, ranging from 4.5 to 9 centimeters. Petiole not preserved. Midvein stout and prominent on the under side of the leaf. Lateral primaries one on each side, opposite, stout and prominent, diverging from the midvein at acute angles at a greater or less distance above its base, ascending and dying out subparallel to the lateral margins one-half or two-thirds the distance to the tip. Secondaries mediumly stout, alternate to subopposite, 3 to 5 pairs, diverging from the midvein at angles of 45 degrees or less, ascending in regular sweeping curves, camptodrome.

From the outer side of the lateral primaries there are numerous, stout, regularly and closely spaced, camptodrome secondaries which diverge at acute angles and are subparallel. Tertiaries well marked, comprising closely spaced and mostly simple veins at right angles to the primaries and secondaries.

This is a type of Tertiary leaf which has frequently been referred to the genus *Ficus*, as for example in the case of the *Ficus mississippiensis* group of

[13] Engelhardt, H. Abh. Senck. naturf. Gesell. **19**: 32, pl. 7, fig. 9, 1895.

the Eocene in the United States,[14] but which probably is not related to *Ficus*. It is also very similar to the leaves of entire Sterculias. Several or all of these may profitably be compared with the modern species of *Hernandia*.

The present fossil form is represented by very incomplete material from Station 27 N., 2 E., but is better known from more complete material from La Victoria, State of Zulia, Venezuela, from which the foregoing description is largely drawn. The specific name is in honor of Jas. A. Tong, one of the collectors of the Venezuelan material.

This species may be matched by the leaves of the existing *Hernandia guianensis* of northern South America. The genus contains ten or a dozen existing species of climbing shrubs in the tropics of both hemispheres and is not otherwise known in the fossil state.

Family LAURACEAE
Genus PERSEA Gaertner fils
Persea coriacea Engelhardt
Plate 2, Figure 2

Persea coriacea Engelhardt, Abh. Senck. naturf. Gesell. **19:** 26, pl. 6, figs. 3, 4, 1895.

Berry, U. S. Natl. Mus. Proc. **75,** art. 24, p. 9, pl. 5, fig. 3, 1929.

The material upon which the present identification is based indicates a leaf somewhat larger than the type, but in view of the well known variation in size of the leaves in individual species of this genus this is not a serious factor.

The species was described from the Tertiary of Santa Ana in Colombia and was compared by its describer with the existing *Persea rigida* Nees—a Brazilian species. It was subsequently recorded from Leiva, Department of Boyaca, Colombia. To me it seems more like the leaves of the existing *Persea gratissima* Gaertner found from Mexico and the Antilles to eastern Bolivia, and now cultivated in all tropical and subtropical regions.

Engelhardt described several large and rather similar fossil leaves from Colombia, referring them to several species of *Nectandra* and *Persea*, and it is almost if not quite impossible to separate them in any objective way.

The age of the flora found near Santa Ana in Colombia has never been determined beyond its being of Tertiary age, although it is certainly not older then Miocene.

Occurrence: Station 35 S., 25 W.

Genus MESPILODAPHNE Nees
Mespilodaphne colombiana Berry, n. sp.
Text-figure 2, No. 1

Leaves of medium size, oval in outline, widest medianly and tapering about equally distad and proximad. Apex abruptly pointed. Base broadly cuneate,

[14] See Berry, E. W. U. S. Geol. Survey Prof. Paper 131, pp. 9–12, 1922.

minutely decurrent. Margins entire and evenly rounded. Texture subcoriaceous. Length between 7 and 8 centimeters. Maximum width about 3 centimeters. Petiole stout, about 1 centimeter in length. Midvein stout, prominent, curved. Secondaries stout, prominent, 7 or 8, somewhat irregularly spaced and mostly alternate pairs they diverge from the midvein at angles around 45 degrees, are regularly curved, ascending, and die out as diminishing arches parallel with the margins. Tertiaries well marked, percurrent across small areas and inosculating over larger ones; where the secondary spacing is wider than the average a subsecondary may intervene.

Of course one cannot be too certain in the generic identifications among the Lauraceae, and I have seen Perseas very similar to the present form, but try to be consistent with the practise laid down in my studies of the Eocene floras of southeastern North America.

I find it objectionable to follow the usage of modern systematists and lump *Oreodaphne* and *Mespilodaphne* in one genus (*Ocotea*).

Occurrence: 27 N., 2 E.; 19 N., 2 W.; 35 S., 25 W.

Order MYRTALES
Family MYRTACEAE
Genus EUGENIA Linné
Eugenia comparabilis Hollick

Eugenia comparabilis Hollick, Bull. N. Y. Bot. Garden **12**: 310, pl. 8, figs. 2–5, 6b, 1924; Berry, Johns Hopkins University Studies in Geology, No. 6, p. 119, pl. 9, figs. 1–5, 1925; Hollick, Sci. Survey of Porto Rico. vol. 7, pt. 3, p. 216, pl. 55, figs. 5b, c; pl. 79, figs. 3 c, d; pl. 80, fig. 1, 1928.

This species is a common element in the porcellanite of Siparia and the Forest Sand of Trinidad, B. W. I., and in the Collazo shales of the Lares district in Porto Rico. Hollick could reach no more definite conclusion in regard to the Collazo shales than that they were Lower Middle Tertiary in age, but I should say that this single species, if correctly identified, proves their Miocene age.

Occurrence: Station 27 N., 2 E.; 19 N., 2 W.; 35 S., 25 W.

Family LECYTHIDACEAE
Genus COUROUPITA Aublet
Couroupita santanderensis Berry, n. sp.
Plate 2, Figure 3

Leaves of medium size, oblong-ovate or slightly oblong-obovate, abruptly pointed at both ends, the base slightly narrower than the tip. Margins entire. Texture coriaceous or subcoriaceous. Length about 14.5 centimeters. Maximum width about 4 to 4.5 centimeters. Petiole missing, obviously stout. Midvein stout, prominent, slightly curved. Secondaries thin, prominent numerous subparallel; they diverge from the midvein at wide angles which de-

crease distad at regular intervals for the most part and are camptodrome. Tertiaries mostly obscured, a few percurrent ones visible. Where two secondaries are more widely spaced there will be an intermediate subsecondary and this may occur once or twice in a single leaf.

The genus contains ten or a dozen existing species of trees ranging from the Lesser Antilles and Central America through northern South America to eastern Peru and south central Brazil. The only other fossil form known to me is *Couroupita ovata* Hollick and Berry[15] of the Pliocene of Bahia, Brazil. Both may be compared with the leaves of *Couroupita guianensis* Aublet and *Couroupita surinamensis* Martius of northern South America.

Occurrence: Station 35 S., 25 W.

Order PERSONALES
Family VERBENACEAE
Genus AVICENNIA Jacquin
Avicennia miocenica Berry, n. sp.
Plate 3, Figures 1–3

Leaves under the average size of those in the existing black mangrove; variable in form, being narrowly ovate, broadly lanceolate or sometimes slightly obovate. Apex varying from acuminate to bluntly pointed. Base rounded to rather narrowly cuneate. Margins entire. Texture coriaceous. Length ranging from 7.5 to 8 centimeters. Maximum width ranging from 1.75 to 2.6 centimeters. Petiole not preserved. Midvein stout and prominent. Secondaries numerous, stout, subparallel, camptodrome; their angle of divergence dependent on the form. Tertiaries mostly obsolete.

The genus contains over 30 existing species cosmopolitan in tropical regions on muddy tidal shores. It appears in the lower Eocene of southeastern North America, and the existing black mangrove, *Avicennia nitida* Jacquin is common in the Pleistocene of Trinidad, B. W. I. What is probably a third fossil occurrence of *Avicennia* is a leaf from Santa Ana in Colombia described by Engelhardt[16] as a species of the Myrtaceous genus *Jambosa* Rumphius—an Oriental type. This differs strikingly from *Avicennia miocenica*.

Occurrence: Station 27 N., 2 E.

Order RUBIALES
Family RUBIACEAE
Genus POSOQUERIA Aublet
Posoqueria columbiana Englehardt
Plate 2, Figure 4

Posoqueria columbiana Engelhardt, Abh. Senck. naturf. Gesell. **19:** 40, pl. 7, fig. 8, 1895.

[15] Hollick, A. & Berry, E. W. Johns Hopkins University Studies in Geology, No. 5, p. 90, pl. 10, fig. 5, 1924.

[16] Engelhardt, H. Abh. Senck. naturf. Gesell. **19:** 35, pl. 9, figs. 6, 7, 1895.

This species was described by Engelhardt from near Buga in the Cauca valley, Colombia, from beds of unknown Tertiary age. It was compared with the existing *Posoqueria latifolia* Roemer & Schultes which is still a native of Colombia, ranging from Panama to the Guianas and southward. It is present in some abundance but in a mostly very fragmentary condition at the plant locality 35 South, 25 West.

The genus contains between 5 and 10 species of shrubs or trees in Central and northern South America.

Incertae Sedis
Phyllites sp.
Plate 3, Figure 5

Fragments of a lanceolate leaf without generic characters are present at Station 27 N., 2 E.

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Invasion by Marchantia polymorpha following forest fires

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Botanical literature bearing upon the ecology of the liverworts in North America is decidedly meager. For the most part this literature seems to be confined to short scattered statements and brief notes. The real value of these must remain in more or less doubt until they have been correlated, or materially supplemented by further investigations. It would seem that our bryologists, thus far, have been more interested in the morphology and taxonomy of the Hepaticae than in their intrinsic value or their economic status in the community.

As a whole there is such a limited quantity of real data available that any fair judgment regarding the environmental relationships of these liverworts must, at least for the present, be held in abeyance. The lack of interest thus evidenced in the ecological features relative to this group would seem to be due to a prevailing idea that the Bryophyta as a whole are of only minor biological importance. The evidence upon which this opinion is based is both scanty and inconclusive. More data are required, and as these accumulate it is possible that this view may be changed. The field is an open one, and it is to be hoped that in time some student of this group may be encouraged to engage in its exploration.

Brinkman (1929) has reported briefly on the habitat preferences of certain liverworts. It is pointed out in his paper that these plants seem to have considerable value as ecological guides in the interpretation of forest conditions. He concludes that members of the Hepaticae may be very useful, and that they play an important role as indices of moisture conditions and of the ultimate capacity of forest sites.

Griggs (1933) has made a study of revegetation in the region of Katmai Volcano, in the Valley of Ten Thousand Smokes. Sterile ash thrown up during the eruption of 1912 was found to be entirely free from vegetation when visited in 1919. Later, in 1930, he found extensive areas of this same ash covered with a pure stand of leafy liverworts, so dense as to form a thick matted carpet. The evidence showed that the districts thus invaded had not been contaminated by any flowage of water from surrounding areas and were entirely lacking in humus. Two species, *Lophozia bicrenata* (Schmid.) Dumort. and *Cephaloziella byssacea* (Roth) Warnst., both members of the leafy Hepaticae, were recognized as the sole invaders, and of these two the latter was seemingly the more important. It is stated that "ordinary plants" are unable to colonize undisturbed deposits of pure ash,

apparently because of a lack of nitrogen. The ash in this instance was found to be practically nitrogen-free. By means of culture experiments, Griggs was able to show that *Cephaloziella* "was able to grow, at least for a time, upon media as nearly free from nitrogen compounds as it is possible to prepare." He concludes that these two species are particularly adapted to this environment because of their small need for soil nitrogen.

Two recent papers by Torrey (1932) were published with the object of recording the early invasion, and seemingly uncontested spread, of *Marchantia polymorpha* over areas denuded of vegetation by forest fires. In the first of these he reports the finding "of large, widely spreading mats of the liverwort *Marchantia polymorpha*, upon thin soil barely covering the ledges, after an almost complete destruction of the previous vegetation" by an extensive forest fire during the preceding autumn. This occurred on the south end of Kittatiny Mountain in Warren County, New Jersey.

In his second equally brief article Torrey quotes from a letter in which W. W. Diehl, of the United States Bureau of Plant Industry, reports having observed this same species of liverwort "in some places covering an acre or more" within an area that had been burned over the previous year. The locality in this case was on Old Rag Mountain, in Virginia. In this same article it is also mentioned that a similar phenomenon had been observed on Long Mountain, in the Harriman section of the Palisades Interstate Park, west of Bear Mountain in New York. No data are given concerning the general conditions of these several habitats. One is led to believe that the burning over of the areas is considered the chief contributory cause of the phenomenon.

This recently reported pyrophilous character of *Marchantia* is not an unknown condition, but one that seems to have escaped prominent mention in the literature. Previously, for example, we find that Durand (1908), in describing the usual habitat of *Marchantia polymorpha*, says that it grows commonly on damp soil in ravines or along wood-roads. But to this statement of usual occurrence, he adds that its best development is reached on damp burned soil. By way of illustration he cites a visit made to a "burntout swamp several acres in extent in which the ground was nearly completely covered with luxuriant thalli to a depth in some places of several inches."

These reports regarding *Marchantia* have been of special interest to me because of similar occurrences that I have observed in the western portion of the United States. Such phenomena are not uncommon, according to my experience, in the mountainous regions of western Montana, particularly in that portion west of the continental divide. There, however, whenever I have found *Marchantia polymorpha* overspreading large areas of

burned-over soil, distinctive humidity and soil conditions were found to prevail.

This pyrophilous nature of *Marchantia* was first strikingly brought to my attention in July of 1924 while I was engaged in making a survey of timber diseases in the Montana state forest north of the town of Whitefish, in Flathead County. This forest area includes Stryker Ridge and the adjacent country of the Stillwater and Whitefish River drainage, and is located in the northwestern portion of the state but a few miles south of the Canadian border. It was the seemingly unusual extent of the area occupied, as well as the nature of the habitat, that attracted my attention.

Subsequently I observed other localities where a similar condition appeared. The best of these was in the valley of the Belmont, a tributary of the Blackfoot River, in the extreme eastern portion of Missoula County. A third instance, also worthy of note, was observed in the valley of one of the upper forks of Dead Man's Gulch, in the Bitter Root Mountains, in the extreme southern portion of Missoula County.

A fourth circumstance was found in the Mission Mountains, on the east side of Flathead Lake, in Lake County. This was in a locality where the fire had occurred several seasons previous to my visit. The conditions in this case had advanced to a point where they were of a much less pronounced character than in the three previously mentioned. The inroad of other plant life had materially changed the scene, and while *Marchantia* was still plentiful other plants were interspersed with it. Conditions were such, however, that one could easily look back through the changes that had taken place and, in the light of conditions observed on Stryker Ridge, the Belmont and Dead Man's Gulch, see the steps by means of which the change had progressed.

The instances previously reported by Torrey from the eastern states, while in mountainous districts, occurred at a comparatively low altitude. He tells me that his Kittatiny Mountain site was at an altitude of from 1,200 to 1,450 feet while that on Long Mountain was at from 800 to 1,100 feet. My western examples occurred at from 3,500 feet to approximately 6,500 feet elevation. The Stryker Ridge site was located at an elevation of somewhere between 3,500 and 3,800 feet. That on the Belmont and the one in the Bitter Root Mountains were both at an elevation of approximately 4,500 feet. There is no intention to assume anything exceptional for these elevations as they are within the perfectly normal range for *Marchantia* in the region under consideration. The highest site in which I observed the pyrophilous habit was that seen in the Mission Mountains. This was at approximately 6,500 feet elevation. It seems doubtful to me if altitude, within reasonable limits, is of any special significance as a deter-

mining factor in the distribution of *Marchantia polymorpha*, though naturally a matter of general interest. The lower river valleys in that portion of Montana situated west of the Continental Divide are at an approximate elevation of 3,000 feet, and this species is quite prevalent in the vicinity of shaded forest streams from that altitude to near the upper forest limits.

The features held in common by the Stryker Ridge, Belmont, and Dead Man's Gulch sites were the invasion, growth and spread of *Marchantia polymorpha* over an area of unusual size, and to the exclusion of other plants, under strikingly similar environmental conditions. The sites in these three instances were located in protected pockets among steep-sided mountains. They had been completely burned over during the period of fire hazard the year preceding my observations. The physical properties and humidity conditions of the soil were practically identical.

The Mission Mountain site, while not in one of these protected mountain pockets, presented otherwise essentially similar features. It was located in a wide saddle, between two mountain peaks, that extended from a point looking down upon the Swan River Valley on the east to one overlooking the Mission Valley on the west. It was short, however, as the steep opposing mountain slopes to the north and south were not far distant from one another. The side of the saddle toward the Mission Valley had been dammed by a morainal deposit, and as a result a well-protected high-altitude lake had been formed. Becoming gradually filled and changed into a marsh-meadow, its soil and humidity characteristics were not essentially different from those of the mountain pockets of the other localities.

The conditions at Stryker Ridge were typical of the several cases that came under my observation. The vegetation of this site, which included somewhat over two acres, and for some considerable distance about, had been severely burned and apparently destroyed. Beyond this the timber destruction must have included about one hundred acres. What had been previously a closely protected mountain marsh-meadow inhabited by the usual grasses and their associates had had these replaced by a dense matted growth of *Marchantia polymorpha*. In looking over the situation there seemed to have been two important factors centributing to the phenomenon, if we may call it such, of *Marchantia* invasion. The peculiar environmental conditions and the morphology of the hepatic seem to have been in close harmony with one another.

One finds many instances of these mountain meadows of varying size, closely surrounded by steep, densely forested hillsides, forming secure pockets among the mountains of the northwest. All of these pocket meadows show evidence of having been at one time the location of small

mountain lakes. These were slowly filled during the course of years. The resulting accumulation is composed, to a considerable depth, of the remains of marsh plants, and above these of meadow plants. These plant remains are mingled with silt and a large amount of fine gravel washed from the steep surrounding hillsides. A considerable quantity of this latter material is brought down by snow slides and the soil slides that habitually occur during the alternate freezing and thawing of spring. The resulting mixture that fills up the lake forms a soil porous enough for good aeration and drainage but with a sufficient quantity of fibrous humus to ensure also a good moisture-holding capacity.

Deep winter snows collect in these pockets and, due to the protection afforded, last later in the spring than the snow on the surrounding slopes. With the melting of this deep snow deposit, and contributions from the higher snow fields, these areas become flooded and remain in a more or less marshy state until early summer. The last rains of spring occur in this region during the early part of June, and no more may be expected until the latter portion of September. The few thunder showers of this summer period are fleeting and furnish comparatively little lasting moisture. The excessively moist period of spring is thus followed by a summer of drought.

The area covered by the growth of *Marchantia* was comparatively level. Despite the violence of the fire, apparently there had been sufficient moisture in the soil at that time to prevent the entire destruction of humus. The surface was thoroughly burned over, but no deeply penetrating "ground fire" persisted to cause, as frequently happens during serious fires, the utter destruction of this necessary soil component. While comparatively level there was, however, provision for efficient but slow drainage. A small stream, with its surface a foot or so below the general ground level, flowed from the upper to the lower end of the meadow.

Marchantia polymorpha is not an uncommon plant within the northern Rocky Mountain region, especially in the vicinity of the numerous forest streams. The "seeding" of the area in question may easily have occurred from plants growing along the stream banks either above or below the burned over meadow.

Spore dispersal is accomplished by means of air currents. In the narrow mountain valleys of this vicinity air drainage is very pronounced and regular in its flow. Breezes habitually blow down the canyons during the night and early morning hours, then reverse and flow upward throughout the day and early evening. As these breezes are regularly recurring, and often of considerable strength, plants above or below the fire area may have contributed their spores to the denuded tract. Spore distribution normally takes place prior to the season of fall rains. It is evident from the

densely matted growth produced that this "seeding" must have been followed by a period of rapid development. The moist nature of the denuded soil during the early autumn and the naturally reduced competition were favorable factors.

With respect to its reproductive period *Marchantia* is decidedly hydrophilous. The organs of reproduction are able to carry out their activities only in the presence of moisture. The antherozoids are motile, and the plants are heterothallic. As a consequence plants of this species are not found except in localities where moisture is plentiful at the requisite season.

On the other hand, *Marchantia polymorpha* is vegetatively xerotherous. This is a decisive factor in its ability to maintain itself in this mountain area. Throughout this region, as I have already mentioned, dry periods of about three months duration normally occur as a seasonal characteristic between June and September. Numerous liverworts and mosses possess this xerotherous habit, an essential to them because of their custom of forming a thin surface layer without material soil penetration.

The quantitative relationship of solutes in the soil to the determination of its habitants is known only to a very limited extent, though admittedly an important factor. Seaver and Clark (1912) have shown that the soluble matter in soils may be increased materially with heating. They have also shown that certain flowering plants are retarded in their growth by this concentrate, but that cryptogamous plants, with their ability to adapt themselves to nutrients of a comparatively high degree of concentration, may respond favorably to such an environment. While this is particularly true of numerous well-known species of fungi, it is also a recognized feature of certain Bryophyta, notably among the mosses. It would seem that *Marchantia polymorpha* may also be included within this category. Seedlings of *Pinus contorta*, *Epilobium angustifolium* and other seed plants characteristic of the floras of burned areas had become established on the adjacent well-drained slopes but had not invaded the marsh-meadow area. The line of demarcation between the *Epilobium* and *Marchantia* formations was very sharp. This condition could not be classed as an exception for, it must be emphasized, the Stryker Ridge, Dead Man's Gulch, and Belmont sites were all similar in this respect.

It will be readily seen that conditions in the several localities I have mentioned were particularly adapted to "seeding" by *Marchantia*, and to the subsequent growth of this plant. If the seeds of other plants present in the surface soil had been killed by the fire early competition would have been minimized. Even if these were not entirely disposed of, their development was, without doubt, inhibited because of the factor just mentioned above. The extensive growth of fireweed and seedlings of lodgepole pine

upon the surrounding slopes of this confined area could hardly be accounted for unless there had been a distribution of their seeds over the entire area. It would seem that we have here very definite evidence and good cause for assuming, in the case of these recognizedly pyrophilous plants, growth inhibition in the burned-over marsh-meadow area.

On the Mission Mountain site of several years standing herbaceous and shrubby flowering plants had become interspersed about the area. These were largely disposed as colonial bays and islands. It is possible that some of these were remnants of the former flora but, from their age and disposition, more probably represented a slow invasion of the locality.

Mosses, of which the genus *Funaria* appeared to be the most prevalent representative, were present in some quantity. Members of several other moss genera were seen, but these, for the most part, were of comparatively minor importance. *Polytrichum* was occasional in drier places near the side slopes. As these mosses may be classed among the pyrophilous plants, it would seem probable that they formed the second troop of invasion, and entered after *Marchantia* had effected some slight change in the surface conditions. While these mosses require a certain amount of periodical humidity they do not care for the extreme moisture conditions tolerated by *Marchantia*.

These mosses were generally disposed about the bays and islands of flowering plants, and to some extent appeared among them. Occasional islets of moss alone were present among the *Marchantia*. Wherever these intrusions were observed, the spot was found to possess somewhat less humidity than its immediate surroundings. In some of these instances a boulder was located a few inches beneath the surface, but such circumstances were by no means universal or even in the majority.

A dense stand of young lodgepole pine occupied the mountain slope adjacent to the southern margin, but had not invaded the marsh area. From this slope the fireweed had almost entirely disappeared because of the denseness of the tree growth. The opposite slope to the north was composed of steep rocky cliffs that afforded little security for trees. It was largely barren rock up which the fire had not passed for any great distance.

It seemed apparent that the development of this Mission Mountain area was more backward than might be expected, and there appeared to be two evident reasons for this condition. A small stream flowed through the marsh-meadow in the case of the Stryker Ridge, Dead Man's Gulch, and Belmont sites. In this instance there was no stream present, and drainage was effected by means of seepage through the coarse gravel of the moraine at the western boundary. For this reason drainage would be slower than in these other cases. Below the moraine, on the outer side, the seepage water

accumulated in sufficient quantity to form a small stream that flowed down the mountain side. Because of the general reaction to conditions there was some considerable evidence that here a swamp, rather than a marsh, might be the final result.

The second reason for retarded development was the matter of altitude. At approximately 6,500 feet the growing period of the more restricted flowering plants was much shortened. *Marchantia*, on the other hand, would not be as greatly influenced by this altitude. Associated with this shortening of the seasonal growth period was another factor of some little importance. The meadow lay in the shadow cast by the mountain peak to the south during the middle and warmer portion of the day. This again would have less effect on the *Marchantia* than on the secondary invaders.

The Belmont site was visited a second time two seasons after its burning. Some slight change was being effected, and it was found that grasses were encroaching upon the *Marchantia* along the stream bank. The *Marchantia* was also showing thin spots here and there through the area, and in these localities colonies of moss were found to be developing. In some of the larger of these moss colonies evidence of grass growth was beginning to appear, though in these places such plants were not yet evident in any great quantity. The most pronounced indications of reversion toward the pre-fire condition were seen at the upper end of the area. Here, both near the stream and from either side of it toward the margin of the marsh, grasses were making a determined effort to return. There were no signs of weediness apparent anywhere in the area.

The Lodgepole pines were developing rapidly on the surrounding hillsides, and while *Epilobium* (*Chamaenirion*) was still in evidence it was being gradually crowded out by other growth. Neither the pines nor fireweed had made any progress in the invasion of the marsh-meadow. All evidence was in favor of a rapid reversion to the status quo and a healthy grass land.

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A study of the growth, transpiration, and distribution of the conifers of the Rocky Mountain National Park[1]

OMER E. SPERRY
(WITH NINE FIGURES)

The Rocky Mountain National Park is a prominent forest area of the central Rocky Mountains in northern Colorado. The Park has an area of 405 square miles (U.S.D.I. 1934) and the forest is in its virgin state, undisturbed by man except in the vicinity of roads and trails.

The rates of diameter increase of the conifers presented in this study have been determined from measurements of increment cores taken from approximately one thousand trees. These trees were selected from undisturbed areas which were reached from the established trails and roads within and near the Park. Growth data were secured from excavated and young trees.

In addition to the growth data, transpiration, evaporation, rainfall, and temperature data were secured and are presented to aid in the explanation of environmental conditions. The number and distribution of trees in given areas and the associated woody and herbaceous plants are also considered. These physical and distribution data were secured primarily from established stations which will be discussed in order.

Although ten members of the *Coniferae* grow within the boundaries of the Park, only five are of economic importance due to quantity and uniformity of growth. These five were selected for this study: *Pinus ponderosa* Lawson, the ponderosa pine; *Pinus contorta* Loudon, the lodgepole pine; *Pseudotsuga taxifolia* (Lamarck) Britton, the Douglas fir; *Abies lasiocarpa* (Hooker) Nuttall, the sub-alpine fir; and *Picea Engelmannii* Engelmann, the Engelmann spruce.

METHODS

Diameter measurements were obtained from cores secured with a Swedish increment borer during the summer of 1932. Some cores were also taken during the summer months of 1929, 1930, and 1931. When cores from the latter were used they were corrected so as to involve corresponding growth rings. One core was taken from the north and one from the south side of the chosen tree at breast height, approximately four and one-half feet from the ground line. These were marked n and s, wrapped, and taken into the field laboratory for further examination.

To secure measurements from the cores in the laboratory each was clamped in a specially designed vise and the surface representing the trans-

[1] Contributions from the Department of Botany, University of Nebraska, N. S. No. 97.

verse section was shaved with a sharp scalpel to obtain a clearer view of the growth rings. The growth rings were counted with the aid of a binocular microscope and were separated into ten-year periods, beginning at the cambial end. The thickness of the wood formed in each ten-year period was then measured in millimeters and recorded. After both north and south radii were recorded the thickness of the wood formed during each ten year period on the diameter of the tree was determined.

Height and diameter measurements were secured from the standing trees. Height was determined in feet by use of the Faustmann hypsometer, the stick method, or by estimations from nearby previously measured trees. Diameter measurements were taken at breast height (4.5 ft.) with a diameter tape and recorded in inches.

Soil temperatures were taken with Centigrade thermometers lowered into wooden tubes which were sunk into the soil to the depth of one foot. A large cork was placed over the bulb end of the thermometer for protection and to help govern rapid changes which might occur due to exposure at the time of reading. The tubes were covered with large rocks and insulated above with tufts of grass.

Evaporation data were obtained with round, white bulb Livingston atmometers placed in the various stations so that the bulbs were less than a foot above the surface of the soil.

Transpiration data were obtained by following the scheme of McLean (1919). Test tubes 100×25 mm. were fastened by means of a copper wire to ropes stretched between two trees at ground and five-foot levels. The test tubes were filled with water and the cut shoot, after being severed under water, was placed in the tube. The test tube was filled to about one-half inch of the top and then covered with a film of olive oil to prevent evaporation and to seal the branch as it extended from the water. After this apparatus was set up and a short time allowed for adjustment, the water level in the tube was marked on the outside of the glass. Water was added after periods of exposure with a pipette graduated in cubic centimeters and the amounts transpired were thus recorded. At the end of the exposure period the twigs used were wrapped in waxed paper and taken into the laboratory. Here the needles were carefully removed from the branches and their green weights obtained. The needles were later dried at 105°C. to obtain dry weights. From these figures the amount of water given off in grams per hour was calculated.

Crown projection maps were made of 100×100 foot plots in lodgepole pine, ponderosa pine, and Douglas fir areas. These maps or "crown mosaics" were constructed similarly to those worked out by Burns (1929). The mapping was done by dividing the plot into 10×10 foot squares.

A six-foot pole with six-inch gradations was used as a measuring device to place the tree in its exact location within the plot. Eight radial projections were made to determine the perimeter of each crown. As these measurements were made they were recorded on a scaled field chart in their exact relations. Shrubs and herbs were also recorded as each 10×10 foot plot was being mapped.

THE STATIONS: TREE AND SHRUB DISTRIBUTION: HERBACEOUS PLANTS WITHIN THE STATIONS

Stations were established in typical areas of the lodgepole pine, ponderosa pine, Douglas fir, and Engelmann spruce-sub-alpine fir. Throughout the discussion which follows they will be referred to as the lodgepole pine station, the ponderosa pine station, the Douglas fir station, and the Engelmann spruce station. These stations were located on slopes which drained toward Fall River and within a radius of two miles of our field laboratory.

The lodgepole pine. The lodgepole pine station was located on the north face of Deer Mountain at an elevation of 8725 feet. The ages of the trees of the station ranged from 55 to 65 years; most of those examined critically were 64 and 65 years old. Careful examination of increment cores from a number of Douglas firs at the base of the slope revealed burn scars for 76 and 95 years back. This indicates that the area was burned in 1837 and again in 1856.

The lodgepole pine is the most common tree of the Park. The elevation at which the tree is usually found ranges from 7500 to about 9500 feet. This species sometimes grows in stands so dense that the plants can hardly be classed as trees, resembling rather so many large weeds. Areas of this type have developed through the excellent seeding conditions that follow fires. Mason (1915) has made counts of representative lodgepole areas and has calculated as many as 50,000 live trees per acre with heights of 8 to 10 feet. On another area he counted 101,000 live trees and 7900 dead ones, or an initial stand of 108,900 trees to the acre with heights of about 4 feet. Clements (1910) made counts of 56 trees to the ten-meter quadrat in the area of Longs Peak and Twin Sisters Mountains. This figures more than 50,000 trees to the acre. Stands of this nature are by far too dense and many of the trees are bound to succumb by gradual retardation and suppression.

In the 100×100 foot area of the lodgepole pine station as many as 14 trees were counted in an area 10×10 feet. The stand in the station as a whole was not so dense, however, and the plotted area supported 218 live trees. Five of these were small limber pines, *Pinus flexilis* James, two

Douglas firs, and 211 lodgepoles. This calculates 949 trees to the acre, which is a very good number if evenly distributed. Mason (1915) places the initial seedlings for a good stand at 1500 to 2000 to the acre. The lodgepole pine makes a better pole when the trees grow closely enough together to cause self pruning but not too close to greatly retard the tree growth.

Figure 1 is the crown mosaic map of the Deer Mountain lodgepole pine station. This sketch gives a definite picture of the distribution of the trees and shrubs within the area. The lodgepole crowns actually cover 44.93% of the ground. This could be construed to mean that when the sun was directly above this section of the forest about 55% of the ground would be exposed to the direct sunlight. Even with this large percentage of exposed ground, there is some crowding due to the chance positions of the trees. Measurements of the overlapping area for this station reveal that 2.22% of the 44.93% is again covered by two or more trees.

The distribution of the woody undergrowth found in the station is shown in the crown projection map (fig. 1). The species recorded are kinnikinnick, *Arctostaphylos Uva-ursi*[2]; New Jersey tea, *Ceanothus Fendleri; Jamesia americana;* the wild rose, *Rosa Sayi;* the red currant, *Ribes cereum;* the buffalo berry, *Shepherdia canadensis;* the elderberry, *Sambucus microbotrys;* the mountain snowberry, *Symphoricarpos racemosus;* and the wild gooseberry, *Ribes saxosum*. The Rocky Mountain maple, *Acer glabrum*, although not present within the station, was growing near by. The sprawling juniper, *Juniperus communis*, could be classed as an undershrub and is found in most forest areas at elevations below 9000 feet.

The lodgepole pine station has the least amount of herbaceous growth of any of the stations mapped. The number of species recorded for this station is not extensive, but indicates the types usually found in similar lodgepole pine areas. The species recorded are: *Arnica cordifolia, Chamaenerion angustifolium, Frasera speciosa, Oreochrysum Parryi, Pyrola minor, Solidago missouriensis, Solidago decumbens,* and *Thermopsis divaricarpa*.

The ponderosa pine. The ponderosa pine is the most common conifer in the foothills and at lower elevations. It grows in scattered groves or as isolated individuals, most commonly on the south and west slopes, at elevations ranging from 7000 to 9000 feet.

Our station was located on the gradual south slope of McGregor

[2] The New Manual of Botany of the Central Rocky Mountains by Coulter and Nelson, Plants of Rocky Mountain National Park by Ashton, Trees and Shrubs of Colorado by Longyear, and Check List of the Forest Trees of the United States by Sudworth have been used in the selection of names.

Mountain at an elevation of 8325 feet. The warm south slope, the open uneven-aged stand, and numerous outcrops of boulders found in this area are typical of ponderosa pine habitats. A number of older trees at the station are fire scarred, and a core taken from one of these contained five

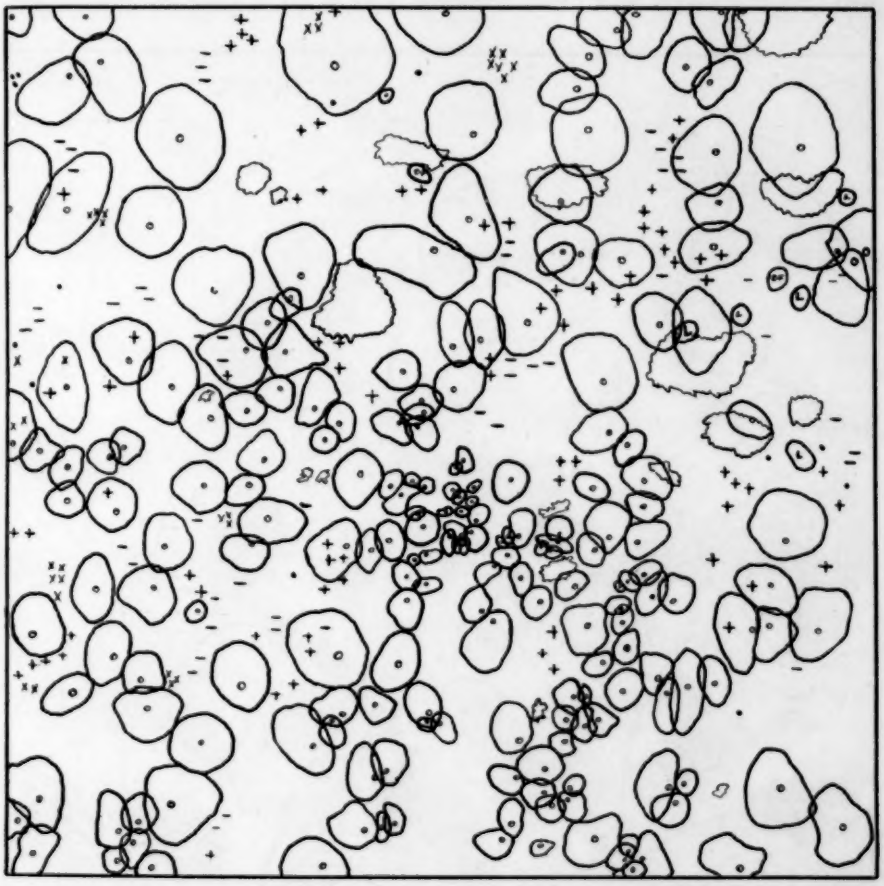

Fig. 1. Crown mosaic of the trees in the lodgepole pine station. The area mapped is 100×100 feet. The small circles indicate the positions of the trunks of the trees, and the irregular lines around these, the perimeters of the crowns. The lighter very irregular areas indicate dwarf junipers. L indicates limber pine, DF, Douglas fir. The symbols are used as follows: +, species of *Ribes;* •, mountain snowberry and elderberry; ×, kinnikinnick; —, wild rose.

resin masses which indicated as many fires or burn injuries. Several trees had open scars at their bases on the north and northeast sides indicating that a ground fire, probably fanned by a north wind, had been severe. The latest date for a fire that could be set from these burn scars was 1790.

In a survey made by the author in 1929 (Sperry, 1934), a ponderosa pine south slope station of 44,000 square feet was found to contain 121 trees or 106 per acre. About 85% of the trees present were ponderosa pines and 69% were over 5 feet tall. Most of the 31% under 5 feet in height were rock growers and older trees. A west slope station of mixed pon-

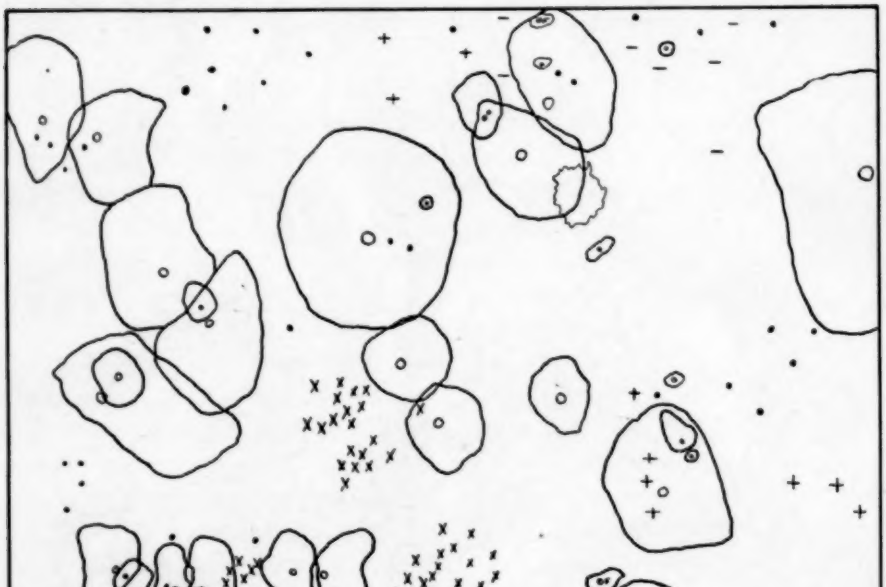

FIG. 2. Crown mosaic of the trees in the ponderosa pine station. The area mapped is 100×100 feet. The small circles indicate the positions of the trunks of the trees, the irregular lines around these, the perimeters of the crowns. Dwarf junipers are indicated by the lighter irregular lines. DF indicates Douglas fir. The symbols are used as follows: •, antelope bush; ×, kinnikinnick; +, species of *Ribes;* −, wild rose.

derosa pine and Douglas fir, 19,750 square feet in area, supported 90 trees or 190 per acre. About 50% of these were ponderosa pine and 15% were young trees less than 5 feet tall.

The McGregor ponderosa pine station (see fig. 2) contained 59 trees or 257 per acre. About 12% of the 59 were Douglas firs and 31% were under 5 feet in height. A number of the lesser trees in this tract were small, twisted rock growers but many more young trees were found than in the station referred to above.

The open forest nature represented by the ponderosa pine station shows the most exposed ground and the least overlapping of crowns. The crowns cover 35.08% of the ground surface and 1.87% is again covered by two or more trees. This overlapping is chiefly due to young trees growing under older trees, as opposed to the overlapping of older trees in the lodgepole pine station.

This station, even with much exposed ground and an open nature, supported the least shrubby undergrowth. The most common was the antelope bush, *Purshia tridentata*. *Jamesia americana* was found in the more protected sites where moisture could be obtained. *Rosa Sayi*, *Ribes cereum*, *Ribes saxosum*, *Ceanothus Fendleri*, and *Arctostaphylos Uva-ursi* were also growing in the mapped area. *Acer glabrum*, although not common on dry south slopes, was present in the vicinity.

The ponderosa pine station had the largest number of herbaceous plants of the three stations mapped. This same relation holds true for the entire ponderosa pine range when compared to that of the Douglas fir and lodgepole pine.

The following are the flowering plants, excluding grasses and sedges, that were present in the mapped area of this station: *Achillea lanulosa*, *Antennaria aprica*, *Apocynum androsaemifolium*, *Arabis Drummondii*, *Artemisia frigida*, *Astragalus flexuosus*, *Erigeron compositus*, *Erigeron flagellaris*, *Erigeron glandulosus*, *Eriogonum umbellatum*, *Erysimum asperum*, *Fragaria ovalis glauca*, *Gaillardia aristata*, *Galium boreale*, *Geranium Fremontii*, *Lithospermum angustifolium*, *Oxytropis bilocularis*, *Pentstemon humilis*, *Potentilla rubricaulis*, *Pseudocymopterus montanus*, *Pulsatilla hirsutissima*, *Sedum stenopetalum*, *Thermopsis divaricarpa*, and *Tithymalis robustus*.

The Douglas fir. The Douglas fir station was established on a slope which drained into Big Horn Creek. The elevation of the station was 8650 feet and the slope faced east of north. The trees of this station presented an average situation for normal development. The lesser trees in the station and in most Douglas fir areas are young trees as opposed to many abnormal and rock growing types which appear as the smaller trees in the ponderosa pine areas.

In an average 50×50 foot plot in an area east of the Park boundary 110 Douglas firs were counted: about 1916 to the acre. Fifty per cent of

these were less than 6 inches in diameter and less than 8 feet tall. In a plot of the same size along upper Big Horn Creek, 44 trees were counted, 766 per acre; 25% of this count were below 6 inches in diameter. The 100×100 foot area of the Douglas fir station supported 128 trees, or 592 to the acre: 23% of these were less than 5 feet in height.

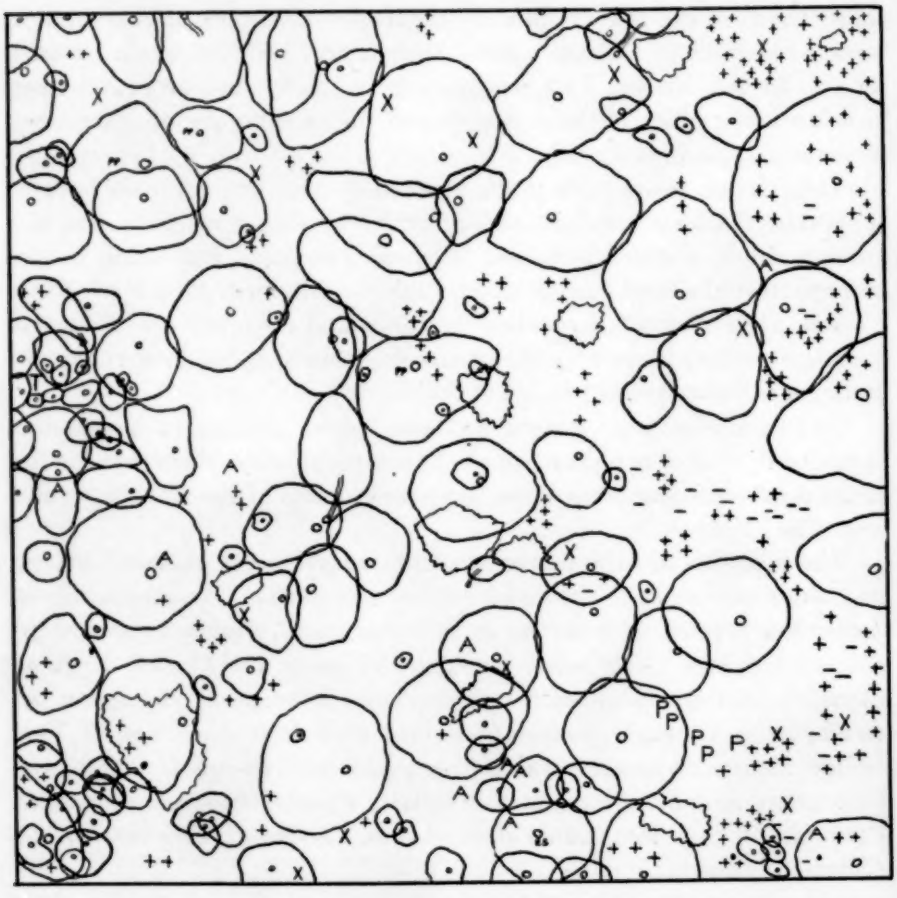

Fig. 3. Crown mosaic of the trees in the Douglas fir station. The area mapped is 100×100 feet. The small circles indicate the positions of the trunks, the irregular lines around these, the perimeters of the crowns. Sprawling junipers are indicated by the lighter irregular areas. PP indicates ponderosa pine; ES, Engelmann spruce. The symbols are used as follows: A, Rocky Mountain maple; P, chokecherry; ×, *Jamesia americana;* +, species of *Ribes;* −, wild rose; •, mountain snowberry.

The crown mosaic (fig. 3) pictures the distribution of all woody plants in the Douglas fir station. The trees of this station shade more ground than was shaded in either the lodgepole or ponderosa pine stations. The

vertical projections of the crowns cover 57.51% of the surface of the station. There was 7.40% of overlapping due almost entirely to younger trees growing in the shade of the established members.

The Douglas fir station supported the greatest amount of woody undergrowth. All woody plants of the two preceding stations except the antelope bush were duplicated here. The larger plants were more numerous, especially the Rocky Mountain maple. The only shrubs found in addition to those mentioned for the other stations were the western chokecherry, *Prunus melanocarpa*, and the arrowwood, *Viburnum pauciflorum*.

The Douglas fir area had the greatest quantity of herbaceous undergrowth. In comparison, the ponderosa pine station had more species but less amount of plant growth. The lodgepole pine station ranked below both these stations in numbers of species as well as quantity of undergrowth. The following are the herbaceous plants, except grasses and sedges recorded for the Douglas fir station: *Arnica cordifolia, Claytonia rosea, Clematis columbiana, Drymocallis fissa, Fragaria ovalis glauca, Galium boreale, Heuchera bracteata, Oreochrysum Parryi, Pentstemon humilis, Saxifraga austromontana*, and *Washingtonia obtusa*.

The Engelmann spruce and sub-alpine fir. The Engelmann spruce station was set up about a mile upstream from the Douglas fir station in an area approximately a quarter of a mile above the lower limits of the spruce-fir belt. The elevation of the station was 9000 feet.

The Engelmann spruce form extensive forests on the slopes and along the mountain streams at elevations ranging from 8500 feet to timberline. The sub-alpine fir also grow within this range and in admixture with the spruce. The Engelmann spruce forest, as a type, reaches its lowest range along streams and waterways. Individuals of the two species are found at elevations as low as 8000 feet.

Seedings and saplings of the spruce and fir are abundant within these forests. lIn an area of 9 square feet in Wild Basin 42 specimens less than 1 foot high were counted and only 6 were productions of the current season. At this rate there could be over 200,000 seedlings and young trees to the acre in addition to the established members.

In a 50×50 foot area in Hidden Valley, 128 spruce and fir were counted or 2230 per acre. Of these 128 trees, 59% were less than 6 inches in diameter, and about 85% of the total were sub-alpine firs; 35% of the 128 were less than 1 foot high (discounting the current year's seedlings) and only 2 of these were Engelmann spruce. In another plot further down the slope very similar results were obtained. The trees in the Engelmann spruce station were not so dense as in the Hidden Valley area and figured only 1390 trees to the acre with 36% less than 5 feet tall, not counting the current season's seedlings.

DIAMETER INCREASE

The study of increment cores taken from the north and south radii of sample trees yield data on the rate of growth after the tree has reached breast height. The figures for the rates of diameter increase are based on the count and measurement of the annual rings from the periphery toward the center. If the core reaches the center, the ring count will give the age of the tree above that level. Decreased diameter growth does not neces-

TABLE 1

The average diameter increase per decade of the five most prominent conifers of the Rocky Mountain National Park. The measurements are in millimeters.

DECADE	PONDEROSA PINE	LODGEPOLE PINE	DOUGLAS FIR	ENGELMANN SPRUCE	SUB-ALPINE FIR
1923–32	15.77	14.38	13.41	14.21	13.48
1913–22	19.75	19.28	20.61	15.67	16.27
1903–12	21.21	20.21	19.49	15.59	17.84
1893–1902	20.47	23.62	17.70	15.85	18.25
1883–92	19.41	26.32	11.55	15.71	16.41
1873–82	15.24	25.30	10.71	13.87	13.65
1863–72	18.80	15.11	11.28	12.77	15.60
1853–62	11.64	11.20	9.52	12.91	14.42
1843–52	17.68	12.17	10.11	11.53	13.73
1833–42	21.06	14.88	12.51	12.97	14.15
1823–32	15.33	12.14	13.24	13.09	14.06
1813–22	13.36	10.26	12.68	12.28	14.74
1803–12	15.48	12.77	16.40	12.75	14.01
1793–1802	15.20	14.95	20.09	13.98	14.39
1783–92	13.78	15.88	20.79	14.94	13.52
1773–82	15.28	9.71	19.55	14.58	10.41
1763–72	15.43	19.94	18.90	12.96	10.13
1753–62	14.35	18.54	16.00	12.74	9.78
1743–52	13.33	16.67	* 8.00	11.76	7.58
1733–42	15.04	16.83	* 5.12	11.68	7.63
1723–32	13.48	*26.75	*16.66	10.02	* 7.67
1713–22	13.56	*31.50	*13.33	10.30	* 7.50
1703–12	13.61	*19.00	*13.33	10.77	*10.50
1693–1702	15.31		*13.00	12.45	* 4.00
1683–92	13.80		*11.33	13.85	* 5.00
1673–82	13.22		*11.33	12.71	* 5.00
1663–72	12.00		*13.33	10.25	
1653–62	13.25		*20.00	* 9.70	
1643–52	10.67			* 6.37	
1633–42	14.00			* 8.00	
Average	15.42	17.74	15.27	13.07	13.52

* Too few trees represented to be included in average.

sarily mean a decrease in volume of wood formed since the layer of wood for each succeeding season is larger and longer. Thus if the diameter increase for any year is as great or greater than for the preceding year, the total volume increment for the later year is greater.

The average diameter increase per decade for all trees measured is presented in table 1. The average decade diameter increments for all trees measured are given as "average" in this table. These averages are not for the same total number of years and range from 180 years for the Douglas fir to 300 years for the ponderosa pine.

Since young trees, under favorable conditions, grow more rapidly in diameter than older trees of the same species, comparisons of growth are made on a basis of diameter-age classes. Classes of trees made in this manner are of an arbitrary nature since growth, either with old or young trees, is a steadily fluctuating variable. Diameter-age classes have thus been created with 100 growth rings (D.B.H.) as the division line so that a more direct comparison in the rates of diameter increase of old and young trees can be made.

The lodgepole pine. The lodgepole pine grew the most rapidly by forming 17.74 mm. of wood on the diameter per decade or 1.77 mm. per year. This is based on the last 200 years (or less) of diameter growth of 254 trees. The average 10-year diameter increase for all lodgepoles with less than 100 growth rings is 24.00 mm. or 2.4 mm. per year. Comparative to this figure, the lodgepole pines with more than 100 growth rings formed 9.49 mm. of wood on the diameter per 10-year period or 0.95 mm. per year. This variation from young to older trees is more marked for the lodgepole pine than for any of the other species studied. The oldest ring count obtained for this species was 239 years but very few trees measured approached the 200 year count. The older trees are either relicts of former stands that were swept by fire or members of an older stand as in the case of a few specimens measured near Bear Lake and in Wild Basin.

The ponderosa pine. The ponderosa pine ranks second to the lodgepole pine in diameter growth with an average of 15.42 mm. of diameter increase per decade or 1.54 mm. per year. Borings from 233 trees were measured as a basis for this determination.

The ponderosa pine and the lodgepole pine have very similar average rates of diameter growth when corresponding periods of time are compared. The last century, 1833 to 1932, netted an average of 18.10 mm. of diameter growth per 10-year period for the ponderosa pine and 19.25 mm. for the lodgepole pine. The preceding century, 1733 to 1832, netted 14.66 mm. for the ponderosa pine and 14.87 mm. for the lodgepole pine, when compared on the same basis. These figures show that the lodgepole

pine has a slightly greater rate of diameter increase than the ponderosa pine and the comparison on a 200-year basis indicates that the former species has a diameter increase of 14.87 mm. per 10-year period as compared to 14.66 mm. for the ponderosa pine.

Ponderosa pine trees less than 100 years old grew more rapidly than the lodgepole pine of the same diameter-age class and an average of 24.57 mm. of wood was formed per decade. The more than 100-year old lodgepole pine trees grew much slower than the ponderosa pines of the same diameter-age rank. The lodgepole formed 9.49 mm. of wood on the diameter per 10-year period and the ponderosa pine formed 14.60 mm. of wood during the same comparative period. The older class of ponderosa pine thus shows a decrease of about 42% in its rate of diameter growth when compared to the younger class of the same species. This corresponding decrease for the shorter-lived lodgepole pine is about 60%.

TABLE 2

Millimeters of diameter increase for trees with more than one hundred growth rings (D.B.H.) and for trees with less than one hundred growth rings (D.B.H.).

DECADE	PONDEROSA PINE		LODGEPOLE PINE		DOUGLAS FIR		SUB-ALPINE FIR		ENGELMANN SPRUCE	
	MORE THAN 100	LESS THAN 100	MORE THAN 100	LESS THAN 100	MORE THAN 100	LESS THAN 100	MORE THAN 100	LESS THAN 100	MORE THAN 100	LESS THAN 100
1923–1932	9.36	22.0	6.65	15.32	9.20	17.78	10.64	19.08	10.41	20.05
1913–1922	14.64	24.14	8.06	20.59	13.31	28.48	12.08	24.52	11.88	25.96
1903–1912	16.21	26.31	8.43	22.48	10.46	29.67	13.33	26.61	13.23	25.66
1893–1902	16.02	26.11	8.79	25.98	11.63	29.60	15.89	29.57	13.29	27.57
1883–1892	15.45	24.44	8.67	30.50	9.62	18.52	13.68	27.24	13.67	27.27
1873–1882	11.26	25.10	10.56	26.07	9.57	17.54	11.35	28.89	12.25	24.30
1863–1872	16.63	23.94	19.41	29.09	10.60	22.20	14.35	30.40	12.35	16.70
1853–1862	9.76	22.08	10.20	16.67	9.43	16.00	14.00	22.33	12.25	19.89
1843–1852	15.63	27.59	10.86	18.00	10.03	16.00	13.73		11.26	16.60
1833–1842	21.00	24.00	13.22	25.25	12.51		14.15		12.97	
Average	14.60	24.57	9.49	24.00	10.67	21.75	13.32	26.06	12.36	22.67

The Douglas fir, Engelmann spruce, and sub-alpine fir. The Douglas fir stands third in diameter growth with an average of 15.27 mm. of diameter increase per decade or 1.53 mm. per year. The sub-alpine fir and Engelmann spruce average much the same with 13.52 mm. and 13.07 mm. of diameter increase per decade, respectively. These calculations are based on tabulations from the measurements of cores from 162 Douglas firs, 151 Engelmann spruces, and 101 sub-alpine firs.

The Douglas fir has the lowest rate of diameter increase for the last 100 years of the 5 trees being considered in this study and ranks closely to the Engelmann spruce and sub-alpine fir in this respect. The diameter growth per 10-year period for the last century, 1833 to 1932, for the Douglas fir was 13.69 mm., the Engelmann spruce was second low with 14.10 mm., and the sub-alpine fir third with 15.38 mm. When the rates of diameter increase for the trees with less than 100 growth rings are compared the same relative rank is held. In this case the Douglas fir averaged 21.75 mm. per 10-year period, the Engelmann spruce 22.67 mm., and the sub-alpine fir 26.06 mm.

The decrease in the rate of growth between the two diameter-age classes for the Douglas fir is about 50%. The Douglas firs with less than 100 growth rings averaged 21.75 mm. of growth per 10-year period and the older trees averaged 10.64 mm. The average diameter growth for the alpine fir with more than 100 growth rings was 13.32 mm., and for the Engelmann spruce of the same class 12.36 mm. Table 2 is a tabulation of the less than 100 growth ring and the more than 100 growth ring diameter-age classes of the five species considered. The height and diameter measurements of the standing trees considered above are summarized in table 3.

TABLE 3

Average, maximum, and minimum heights and diameters for all trees measured and included in diameter growth figures.

SPECIES	PONDEROSA PINE	LODGEPOLE PINE	DOUGLAS FIR	ENGELMANN SPRUCE	SUB-ALPINE FIR
NUMBER OF TREES	233	254	162	151	101
Average height	33.60 ft.	33.53 ft.	37.33 ft.	48.70 ft.	43.61 ft.
Maximum height	92.00 ft.	85.00 ft.	80.00 ft.	100.00 ft.	100.00 ft.
Minimum height	10.00 ft.	15.00 ft.	12.00 ft.	12.00 ft.	10.00 ft.
Average diameter	13.33 in.	6.49 in.	11.28 in.	12.19 in.	8.62 in.
Maximum diameter	41.20 in.	19.50 in.	48.00 in.	34.25 in.	19.25 in.
Minimum diameter	2.50 in.	2.00 in.	2.25 in.	2.50 in.	2.25 in.

HEIGHT GROWTH

A number of small trees were examined to determine the rate of height growth for trees less than 4.5 feet in height. In addition to these, three older lodgepole pines were excavated and examined critically for rates of height growth. The data secured from the seedling and sapling study are presented in table 5. In most of these ring counts microscopic mounts had to be made due to the narrow rings.

The lodgepole pine. The lodgepole pine, with its ability to invade areas

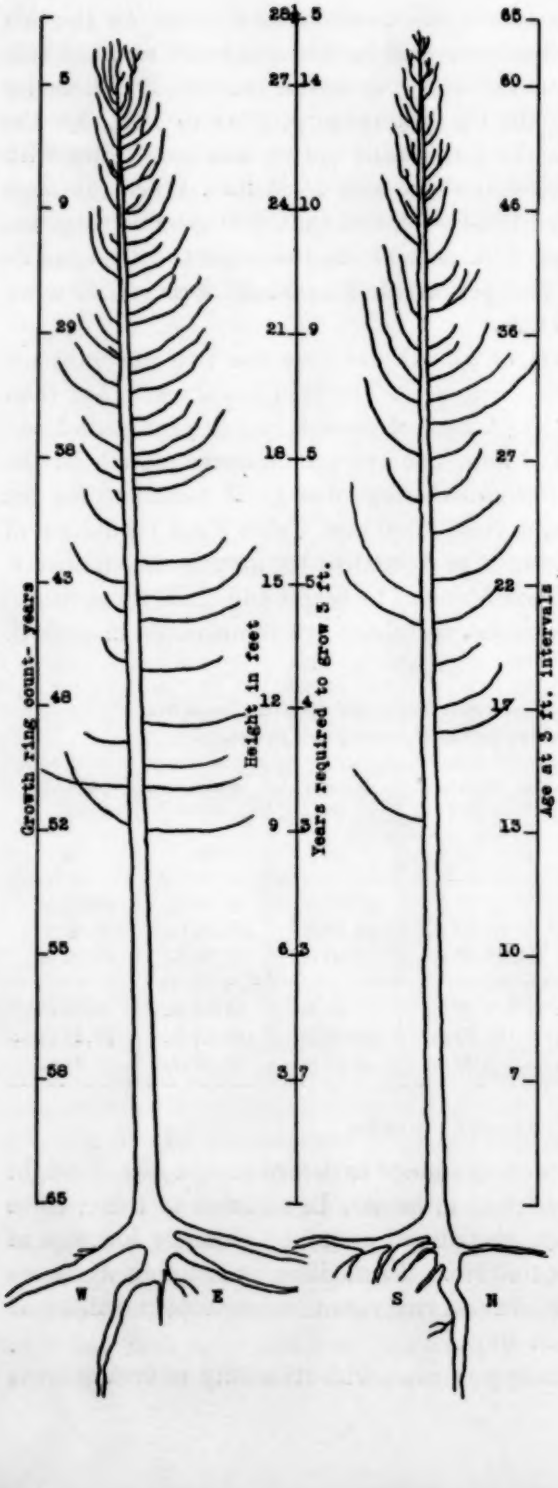

Fig. 4. A diagrammatic longisection of a lodgepole pine tree from north-south and east-west views to show the position and relative size of roots and branches. All parts are drawn to the same scale.

deforested by fire, has the most rapid rate of growth. Figure 4 shows a diagrammatic longisection of a lodgepole pine from both north-south and east-west views. This figure shows the behavior of one of the three average trees which were dug out of the lodgepole pine station. Ring counts were made for each tree from the transition root-stem zone at the ground line upwards at 3 foot levels. The tree represented in this sketch grew very slowly until it had attained a height of three feet, the rate of growth was then more than doubled until a height of 12 feet was reached, after which the rate decreased as the tree approached its present state of maturity. All the trees thus examined showed this same general tendency in their rates of height growth (see table 4).

TABLE 4

Ring count at three-foot levels of three lodgepole pine trees.

LEVEL IN FT.	RING COUNT—YEARS			
	TREE 1	TREE 2	TREE 3	AVERAGE
Ground	65	64	64	64.3
3	58	57	59	58.0
6	55	50	57	54.0
9	52	42	55	47.3
12	48	38	49	45.0
15	43	33	43	37.7
18	38	24	34	32.0
21	29	16	6	17.0
24	19			
27	5			
Tree ht. in feet	27.58	25.58	22.0	25.0

Seedling establishment and growth are essential to the continuation of any forest area. If the trees present cannot reestablish themselves the stand will be replaced by a more adaptable species. This situation exists in the case of the lodgepole pine which seeds itself most effectively in open exposed areas. If the stand is dense or moderately so, shade is undoubtedly the factor in the failure of the lodgepole to reestablish itself. This intolerant nature has been shown by Korstian (1925) in the effects of shade on nursery stock. An illustration of the retarding nature of the established forest over seedlings can be made by considering the rate of growth of tree number 22 from table 5. This tree was 55 years old and only 4 feet high, while the older trees, which had become established ten years earlier, averaged about 27 feet in height. The older tree, illustrated in figure 5, required 7 years for the first 3 feet of height growth while the smaller tree netted only 3 inches of height in 7 years. One other small lodgepole, 38

inches high, was examined. This specimen grew 1 inch per year for the first three years and continued at about that same rate until it was over one foot high. After that the rate of growth was gradually retarded and 16 years were required for the second and third feet of height growth.

TABLE 5

Ring count from the ground line upward at three to twelve inch levels to determine rate of growth for young trees. S.F. indicates sub-alpine fir, E.S., Engelmann spruce, D.F., Douglas fir, P.P., ponderosa pine, and L.P., lodgepole pine.

	SPECIES	HEIGHT IN INCHES	DIAMETER AT GROUND LINE IN INCHES	AGE AT GROUND LINE	AGE AT 3 INCH LEVEL	AGE AT 6 INCH LEVEL	AGE AT 9 INCH LEVEL	AGE AT 12 INCH LEVEL	AGE AT 18 INCH LEVEL	AGE AT 24 INCH LEVEL	AGE AT 36 INCH LEVEL	AGE AT 48 INCH LEVEL
1.	S.F.	1.25		5								
2.	S.F.	2.5		11								
3.	S.F.	4.5	.094	10	2							
4.	S.F.	5.0	.187	13								
5.	S.F.		1.63	48	44	40						
6.	S.F.	10.0	.125	36	31	19						
7.	S.F.	12.0	.25	27	20	9	2					
8.	S.F.	24.0	.875	54	35	28	20	17	6			
9.	S.F.	48.0	1.125	80	70	37	34	32	25	18	8	
10.	E.S.	1.75		4								
11.	E.S.	11.0	.271	27	19	12	3					
12.	E.S.	11.0	.25	36	27	12						
13.	E.S.	12.0	.271	23	12	4						
14.	E.S.	36.0	1.125	57	52	48	44	40	20	12		
15.	E.S.	38.0	.875	63								
16.	D.F.	28.0	.562	44	35	25	19	12	7	2		
17.	D.F.	40.0	.875	47	40	32	29	27	25	13	8	
18.	D.F.	50.0	1.25	57	49	40	25	22	15	12	7	2
19.	P.P.	38.0	1.00	31	25	19	17	15	13	9		
20.	P.P.	58.0	1.75	42	38	32	28	27	19	18	10	6
21.	L.P.	38.0	.812	32	29	25	21	19	16	12	3	
22.	L.P.	48.0	1.125	55	48	44	40	36	25	22	9	

The ponderosa pine. The seedlings of the ponderosa pine are very scarce in this area and one seldom finds a current season's seedling. They do occur, however, as young trees are present, but to a lesser degree than seedlings of neighbor species.

One tree 38 inches and one 58 inches high were examined to obtain facts regarding the rates of growth for trees under 4.5 feet in height. The shorter tree was 31 years old and the taller 42 years, according to ring

count. On the average, 5 years were required for the first 3 inches of height growth, 6 years for the second 3 inches, 3 years for the third 3 inches, and 1.5 years for the fourth 3 inches. Thus, there was an increase in the rate of growth as the trees became established. The first foot of height was reached during the fifteenth and sixteenth growing seasons. This acceleration in the rate of growth continued and the second foot of height was reached during the twenty-second and twenty-fourth growing seasons.

Fig. 5. Seedlings of *Abies lasiocarpa*. A, cotyledonary stage; B, two years old; C, early in third growing season; D, four years old. These specimens were collected in the Engelmann spruce station.

The Douglas fir. Three trees were obtained to illustrate the rate of growth for young Douglas firs. They averaged 37 inches high and 47 years old. The average first 3 inches of height was attained in 8 years, the second 3 inches in 9 years, the third 3 inches in 8 years, and the fourth 3 inches in 4 years. The first foot of height was reached in 29 years and the second in an additional 11.3 years. The seedlings, thus, did not exhibit the rapid and steady increase in the rate of growth that the ponderosa pine did.

The Engelmann spruce and sub-alpine fir. The sub-alpine fir examined averaged 8.83 years in attaining the first 3 inches of height, 13.4 years for the second 3 inches, 5.67 years for the third 3 inches, and 2.5 years for the fourth 3 inches. The slow rate of growth of the sub-alpine fir is illustrated in figure 5 which is a photograph of four seedlings, 1, 2, 3, and 4 years old. The Engelmann spruce seedlings examined grew faster than the above sub-alpine fir and averaged 16.75 years for the first 6 inches of height growth.

ENVIRONMENTAL CONDITIONS

The only available data on rainfall and temperature were those collected at the Colorado Public Service Station in cooperation with the United States Weather Bureau. This station is located on the valley floor at the base of the south slope of McGregor Mountain about three-fourths mile below the location of the ponderosa pine station. The records were not complete for every month from 1928–1932 due to a change of station location and a loss of some records.

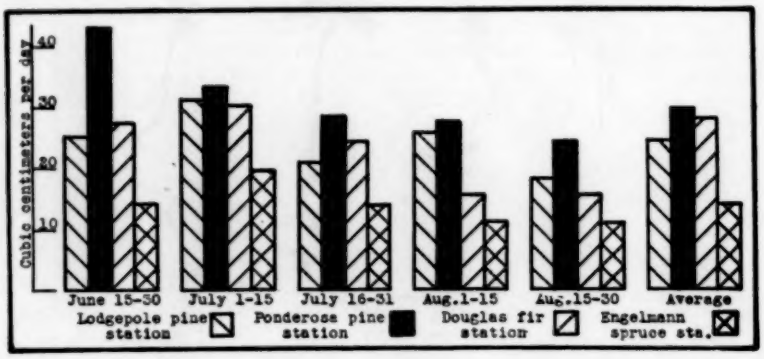

Fig. 6. A graphical representation of evaporation from atmometers during fifteen-day periods in the four stations.

The average annual rainfall recorded for the five-year period (see table 6) was 12.99 inches. Since these records were taken near the ponderosa pine station we may conclude that the species in this area receive about 13 inches of rainfall annually. The most moisture falls during the months of March, April, July, and August. January and December are the driest months of the year.

The lowest temperatures recorded at this station were in March, but the cold periods were usually of shorter duration than those of the three or four preceding winter months. The average maximum and the maximum high temperatures for June, July, and August showed little variation. July had the highest average maximum temperature and August the greatest daily range.

Evaporation data, measured by means of Livingston white bulb atmometers, were obtained at the four stations during the summer months of 1932. These data are illustrated graphically in figure 6. Evaporation is recorded in cubic centimeters per day; 15-day periods are compared. A greater amount of water was lost in the ponderosa pine station than in any of the other stations. The Douglas fir station ranked second, the

lodgepole pine third, and the least amount of water was given off in the area of the Engelmann spruce.

Soil temperatures were obtained only in the Douglas fir and ponderosa pine stations. The temperatures obtained from the ponderosa pine station showed a greater range than those from the Douglas fir station. This same relation existed in the air temperatures. The temperatures at one foot below the surface of the ground averaged 17.30°C. in the ponderosa pine station and 12.30°C. in the Douglas fir station. The maxima were 22°C. and 13°C., the minima in both 11°C. Thus, the greatest daily range in temperature for the ponderosa pine station was 11°C. while only 2°C. was recorded as a maximum range for the Douglas fir habitat.

TABLE 6

Temperature in degrees Fahrenheit, and rainfall in inches for 1928–1932. Records made at the Colorado Fish Hatchery 1928, and at the plant of the Colorado Public Service Company 1929–32.

MONTH	AVERAGE MAXIMUM	AVERAGE MINIMUM	AVERAGE RANGE	MAXIMUM RECORD	MINIMUM RECORD	AVERAGE RAINFALL
Jan.	33.3	14.6	21.1	52.3	0.1	0.20
Feb.	39.7	19.2	21.4	56.0	1.2	0.98
March	41.7	19.1	26.3	55.8	−12.2	2.23
April	54.1	27.5	27.6	68.0	8.3	1.03
May	59.2	31.2	27.7	78.2	15.8	0.98
June	69.3	36.0	31.3	83.0	28.0	0.93
July	77.9	50.9	32.6	88.0	32.5	2.50
Aug.	70.1	42.4	44.8	83.0	35.8	1.02
Sept.	65.6	37.6	28.9	80.0	24.0	0.66
Oct.	57.4	30.0	32.6	74.2	16.0	0.61
Nov.	40.6	19.0	23.9	61.7	− 6.7	1.55
Dec.	37.1	15.3	24.2	56.0	− 0.25	0.20
					Total annual rainfall	12.99

POTOMETER STUDIES

The cut shoot (potometer) type of phytometer as described under Methods was used in this study. The volume of transpiration is very difficult to measure accurately since any man-made device for such attempts removes the tree from its normal growing conditions. Thus, potometer records are not true measures of transpiration and are used as comparative measures for the trees concerned. Shoots were exposed for short periods because longer periods cause a decrease in the rate of transpiration due to a gradual blocking of the vascular system (Maximov, 1929). The most valuable information from such an instrument, according to Maximov, is obtained just after the cutting of the shoot.

The potometers were run at approximately two-week intervals during the summer of 1932, beginning June 16. The shoots were placed in the same positions in the same stations at each experimental period which ranged from 6 to 7.8 hours. Before setting up the experiment, trees from which the cut shoots were to be taken were located and marked. The cut shoots for all three stations were obtained from the same side of the same tree and as nearly as possible from the same level. The shoots were first taken to the lodgepole pine station with the cut ends in water and the potometers set up as previously described. After installing the apparatus in the lodgepole pine station, shoots were taken from this station to the ponderosa pine and Douglas fir stations and similar installations were made. By using a saddle horse less than two hours were needed for this

TABLE 7

The amount of water lost from potometers on June 16. The calculations are based on cubic centimeters per gram of green leaf per hour and per gram of dry leaf per hour. P.P. indicates ponderosa pine, L.P., lodgepole pine, and D.F., Douglas fir.

	SPECIES	TIME IN HRS.	CC. TRANS.	GREEN WT. G.	CC./G./HR. GREEN WT.	DRY WT. G.	CC./G./HR. DRY WT.
Lodgepole Pine Station							
5-foot level	P.P.	6	24.8	60.9	.068	32.7	.126
	L.P.	6	8.7	14.1	.103	7.2	.201
	D.F.	6	9.0	27.4	.054	14.1	.106
Ground level	P.P.	6	25.9	64.9	.067	33.9	.127
	L.P.	6	10.1	14.2	.119	7.4	.227
	D.F.	6	6.8	39.9	.028	21.6	.052
Ponderosa Pine Station							
5-foot level	P.P.	7.5	15.4	20.8	.099	10.3	.199
	L.P.	7.5	15.6	10.7	.194	4.7	.442
	D.F.	7.5	12.8	23.8	.072	11.5	.148
Ground level	P.P.	7.5	18.2	14.25	.170	7.1	.342
	L.P.	7.5	7.5	5.2	.192	2.3	.436
	D.F.	7.5	12.9	19.4	.089	9.4	.183
Douglas Fir Station							
5-foot level	P.P.	7	10.4	15.5	.096	10.3	.144
	L.P.	7	10.2	11.85	.118	4.7	.310
	D.F.	7	5.6	17.0	.044	11.5	.070
Ground level	P.P.	7	8.2	15.65	.075	7.1	.165
	L.P.	7	9.2	10.7	.123	2.3	.571
	D.F.	7	4.0	13.05	.044	9.4	.061

procedure. Water was added and the apparatus taken down in the same order. This allowed about the same amount of time for transpiration in all three stations. The transpiration data obtained for the six periods are presented in tables 7 to 12.

Wet and dry bulb readings were taken with a cog psychrometer in the three stations on the days that the potometer experiments were run. These readings were not taken at intervals sufficiently close to be of great comparative value. The temperatures were usually the highest in the ponderosa pine station, averaging 67.43°F. at 9:15 A.M. and 67.64°F. at 2:30 P.M. The average in the Douglas fir station was 65.25°F. at 9:40 A.M. and 65.42°F. at 3:45 P.M. The average in the lodgepole pine station was 55.21°F. at 8:45 A.M. and 45.00°F. at 3:00 P.M. The relative humidities

TABLE 8

The amount of water lost from potometers on July 1. The calculations are based on cubic centimeters per gram of green leaf per hour and per gram of dry leaf per hour. P.P. indicates ponderosa pine, L.P., lodgepole pine, and D.F., Douglas fir.

	SPECIES	TIME IN HRS.	CC. TRANS.	GREEN WT. G.	CC./G./HR. GREEN WT.	DRY WT. G.	CC./G./HR. DRY WT.
Lodgepole Pine Station							
5-foot level	P.P.	6	9.7	20.6	.070	8.5	.190
	L.P.	6	5.3	8.25	.107	3.0	.294
	D.F.	6	3.3	9.5	.056	4.1	.134
Ground level	P.P.	6	8.4	23.5	.060	10.1	.139
	L.P.	6	4.6	8.1	.095	2.9	.264
	D.F.	6	7.3	14.0	.087	5.4	.225
Ponderosa Pine Station							
5-foot level	P.P.	6	6.8	13.2	.086	4.3	.264
	L.P.	6	4.25	3.7	.191	1.8	.394
	D.F.	6	5.0	9.5	.088	4.3	.194
Ground level	P.P.	6	6.3	14.0	.075	5.3	.198
	L.P.	6	5.5	8.5	.108	3.4	.271
	D.F.	6	5.1	10.5	.081	4.3	.197
Douglas Fir Station							
5-foot level	P.P.	6	6.7	17.9	.062	7.3	.153
	L.P.	6	3.5	8.4	.069	3.0	.194
	D.F.	6	4.0	9.5	.070	3.7	.180
Ground level	P.P.	6	7.7	15.8	.081	6.1	.210
	L.P.	6	4.1	7.7	.089	3.1	.220
	D.F.	6	3.5	11.0	.053	3.9	.150

were not as constant nor as comparable as the temperature readings. The average low was 39.57% for 3:00 P.M. in the lodgepole pine station and the average high was 49.17% for 3:45 P.M. in the Douglas fir station.

The transpiration figures which follow are based on green weight. Calculations were made for dry weight and are included in tables 7 to 12. The ratio between dry and green weight was very constant and the latter are used in the following comparisons.

TABLE 9

The amount of water lost from potometers on July 18. The calculations are based on cubic centimeters per gram of green leaf per hour and per gram of dry leaf per hour. P.P. indicates ponderosa pine, L.P., lodgepole pine, and D.F., Douglas fir.

	SPECIES	TIME IN HRS.	CC. TRANS.	GREEN WT. G.	CC./G./HR. GREEN WT.	DRY WT. G.	CC./G./HR. DRY WT.
Lodgepole Pine Station							
5-foot level	P.P.	7.8	11.1	14.6	.097	6.9	.210
	L.P.	7.8	8.3	9.2	.115	4.5	.237
	D.F.	7.8	8.6	14.0	.079	5.8	.181
Ground level	P.P.	7.8	9.3	11.0	.108	5.0	.238
	L.P.	7.8	8.4	8.4	.128	3.7	.291
	D.F.	7.8	7.6	11.1	.088	4.6	.212
Ponderosa Pine Station							
5-foot level	P.P.	7.6	15.2	15.7	.127	7.2	.278
	L.P.	7.6	11.4	8.2	.183	3.9	.385
	D.F.	7.6	11.6	21.8	.070	9.1	.168
Ground level	P.P.	7.6	14.9	17.8	.110	8.0	.245
	L.P.	7.6	14.0	6.25	.295	2.9	.635
	D.F.	7.6	13.7	17.3	.104	6.9	.261
Douglas Fir Station							
5-foot level	P.P.	7.4	14.3	21.4	.090	9.7	.200
	L.P.	7.4	12.2	9.8	.168	4.0	.412
	D.F.	7.4	6.5	16.55	.053	7.2	.122
Ground level	P.P.	7.4	10.1	15.2	.090	7.3	.187
	L.P.	7.4	8.5	12.7	.090	5.3	.217
	D.F.	7.4	8.95	21.1	.057	8.9	.136

Transpiration comparisons within the stations. The cubic centimeters of water lost per gram of green leaf per hour at the ground and 5 foot levels have been averaged and figures 7, 8, and 9 constructed. These figures

represent the amounts of water transpired by the three species in the respective stations during the six experimental periods.

Gail (1921) exposed cut shoots of Douglas fir for periods of four hours and found that 2.89 times as much water was lost on the southwest slopes as on the northeast slopes. If we consider the ponderosa pine station as

TABLE 10

The amount of water lost from potometers on August 1. The calculations are based on cubic centimeters per gram of green leaf per hour and per gram of dry leaf per hour. P.P. indicates ponderosa pine, L.P., lodgepole pine, and D.F., Douglas fir.

	SPECIES	TIME IN HRS.	CC. TRANS.	GREEN WT. G.	CC./G./HR. GREEN WT.	DRY WT. G.	CC./G./HR. DRY WT.
Lodgepole Pine Station							
5-foot level	P.P.	6.5	14.0	28.0	.077	12.3	.175
	L.P.	6.5	8.3	10.6	.120	5.0	.254
	D.F.	6.5	5.5	11.5	.074	5.2	.163
Ground level	P.P.	6.5	11.2	22.3	.077	10.2	.109
	L.P.	6.5	7.9	11.6	.105	5.4	.225
	D.F.	6.5	7.4	9.9	.115	4.6	.247
Ponderosa Pine Station							
5-foot level	P.P.	6.5	18.1	24.8	.114	10.7	.260
	L.P.	6.5	18.3	20.2	.139	9.5	.296
	D.F.	6.5	8.6	18.8	.070	9.4	.141
Ground level	P.P.	6.5	16.5	30.5	.083	12.0	.211
	L.P.	6.5	8.0	13.6	.090	6.9	.178
	D.F.	6.5	2.7	15.6	.027	8.0	.052
Douglas Fir Station							
5-foot level	P.P.	6.5	15.4	35.0	.068	16.0	.148
	L.P.	6.5	5.5	10.5	.081	5.0	.171
	D.F.	6.5	6.7	16.2	.064	7.2	.143
Ground level	P.P.	6.5	10.7	27.4	.060	12.6	.131
	L.P.	6.5	4.2	9.8	.066	4.6	.140
	D.F.	6.5	5.3	16.9	.048	8.1	.101

comparable to the above southwest slopes and the Douglas fir station to the northeast slopes, we find 1.31 times as much water lost by the Douglas fir in the ponderosa pine station as in its own station. If the water loss of all shoots is compared, we find 1.44 times as much water lost in the

ponderosa pine and 1.16 times as much in the lodgepole pine as in the Douglas fir station.

Figure 7 shows the amounts of water transpired by the lodgepole pine in the three stations. The lodgepole pine appears to be an extravagant user of water. The response of the lodgepole pine to the conditions of the

TABLE 11

The amount of water lost from potometers on August 13. The calculations are based on cubic centimeters per gram of green leaf per hour and per gram of dry leaf per hour. P.P. indicates ponderosa pine, L.P., lodgepole pine, and D.F., Douglas fir.

	SPECIES	TIME IN HRS.	CC. TRANS.	GREEN WT. G.	CC./G./HR. GREEN WT.	DRY WT. G.	CC./G./HR. DRY WT.
Lodgepole Pine Station							
5-foot level	P.P.	7	12.7	29.9	.061	9.7	.187
	L.P.	7	12.6	15.2	.118	6.3	.277
	D.F.	7	10.2	13.1	.111	6.0	.243
Ground level	P.P.	7	31.5	23.7	.189	9.5	.474
	L.P.	7	10.8	17.3	.089	7.6	.203
	D.F.	7	7.5	12.1	.089	5.3	.202
Ponderosa Pine Station							
5-foot level	P.P.	6.7	20.4	38.2	.079	15.4	.197
	L.P.	6.7	14.3	16.2	.132	7.3	.292
	D.F.	6.7	10.0	21.4	.069	9.3	.160
Ground level	P.P.	6.7	12.9	29.4	.065	12.1	.159
	L.P.	6.7	29.3	21.6	.202	9.0	.486
	D.F.	6.7	11.2	23.1	.072	11.0	.152
Douglas Fir Station							
5-foot level	P.P.	6.7	17.0	24.9	.102	9.4	.270
	L.P.	6.7	14.8	21.2	.104	9.2	.240
	D.F.	6.7	11.3	25.3	.067	11.2	.150
Ground level	P.P.	6.7	16.4	35.8	.068	14.7	.166
	L.P.	6.7	12.0	16.6	.108	7.2	.249
	D.F.	6.7	5.2	19.2	.040	8.6	.190

environment at the three stations is also very marked and in every case the greatest amount of water was given off in the ponderosa pine station. Water lost in the lodgepole pine and Douglas fir stations varied, but the average at the end of the summer was greater in the environment of the lodgepole pine.

Figure 8 places the data obtained from the transpiration of the ponderosa pine in the various stations on a readily comparative basis. With one exception, the greatest amount of water was transpired by the ponderosa pine in its own habitat; the early and late season's losses were

TABLE 12

The amount of water lost from potometers on August 25. The calculations are based on cubic centimeters per gram of green leaf per hour and per gram of dry leaf per hour. P.P. indicates ponderosa pine, L.P., lodgepole pine, and D.F., Douglas fir.

	SPECIES	TIME IN HRS.	CC. TRANS.	GREEN WT. G.	CC./G./HR. GREEN WT.	DRY WT. G.	CC./G./HR. DRY WT.
Lodgepole Pine Station							
5-foot level	P.P.	6	16.5	30.3	.085	12.4	.222
	L.P.	6	11.0	21.3	.086	8.8	.208
	D.F.	6	8.0	21.8	.061	9.3	.143
Ground level	P.P.	6	14.2	23.7	.100	10.5	.225
	L.P.	6	8.1	17.8	.076	8.1	.166
	D.F.	6	7.2	23.8	.050	10.5	.114
Ponderosa Pine Station							
5-foot level	P.P.	6.3	13.0	22.3	.092	9.9	.208
	L.P.	6.3	11.0	21.2	.082	9.7	.180
	D.F.	6.3	6.7	17.9	.059	8.0	.133
Ground level	P.P.	6.3	18.2	22.1	.131	9.5	.304
	L.P.	6.3	18.5	32.8	.089	13.5	.217
	D.F.	6.3	8.6	24.6	.055	10.5	.130
Douglas Fir Station							
5-foot level	P.P.	6.3	16.8	20.2	.132	8.7	.307
	L.P.	6.3	12.0	23.9	.080	10.4	.183
	D.F.	6.3	8.6	19.2	.071	9.0	.152
Ground level	P.P.	6.3	13.4	27.2	.078	11.0	.193
	L.P.	6.3	8.7	30.7	.039	12.7	.109
	D.F.	6.3	5.1	20.7	.039	9.2	.089

greatest in the area of the Douglas fir, and the mid-summer losses were greatest in the lodgepole pine station. The average for the summer was slightly greater in the region of the lodgepole.

The response of the Douglas fir potometers to the three environments is shown in figure 9. The Douglas fir was most conservative in the use of water in its own station. In four out of six experiments, the greatest amounts of water were lost in the ponderosa pine area and on two oc-

casions the most was transpired in the lodgepole pine habitat. The average for the season was slightly greater in the lodgepole than in the ponderosa pine station.

This relative rank of water loss, as measured by potometers agrees in the main with the results of Bates (1923) and Pearson (1924) who used potted seedling phytometers to secure data on transpiration. The findings are also in agreement with Roeser (1932) who used seedlings in water

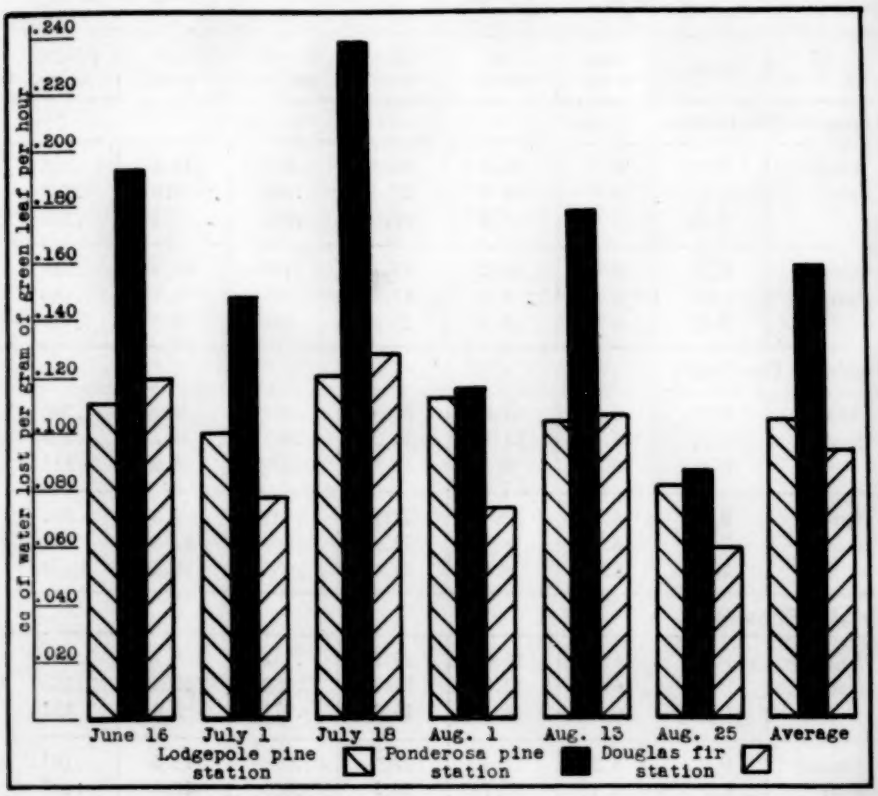

Fig. 7. A comparison of the rates of transpiration of the lodgepole pine in the lodgepole pine, ponderosa pine, and Douglas fir stations.

cultures. Gail and Long (1935) on the other hand found that the rate of water loss for potted lodgepole seedlings failed to exceed the losses recorded for corresponding ponderosa pine seedlings.

When the cubic centimeters of water lost per gram of green leaf per hour by the three species in all three stations are computed, a grand average is obtained of .120 cc. for the lodgepole, .091 cc. for the ponderosa pine, and .0663 cc. for the Douglas fir. This ranking is in agreement with

Bates (1923) in that both the western yellow (ponderosa) pine and lodgepole pine transpired more per tree than the Engelmann spruce and Douglas fir.

Roeser (1932) found that the Douglas fir showed a much smaller in-

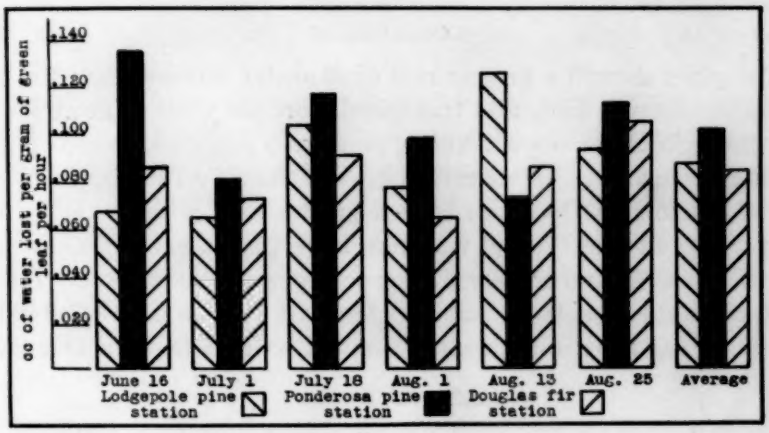

Fig. 8. A comparison of the rates of transpiration of the ponderosa pine in the lodgepole pine, ponderosa pine, and Douglas fir stations.

crease in transpiration in comparison with the other species when the habitats were varied. In our experiments the ponderosa pine fluctuated the least with an average decrease of 16.2% when placed in the lodgepole

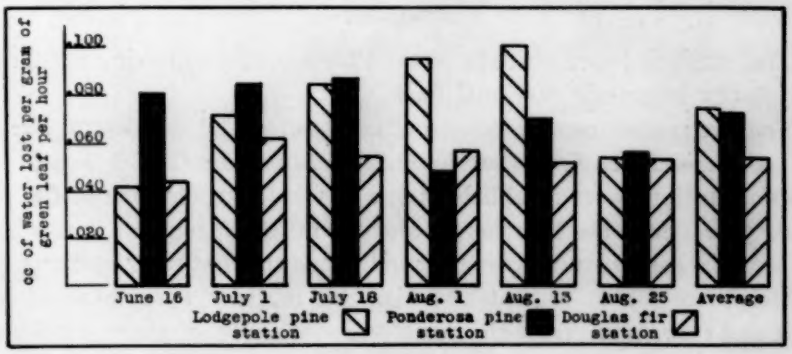

Fig. 9. A comparison of the rates of transpiration of the Douglas fir in the lodgepole pine, ponderosa pine, and Douglas fir stations.

and Douglas fir stations. The Douglas fir ranked second with an average increase of 34.2% in the habitats of the pines. The lodgepole increased its rate of transpiration 52.4% in the ponderosa pine and decreased 8.5% in the Douglas fir station.

The water loss of potometers within the stations is in the same order as water evaporated from atmometers in the respective stations. The potometer records are based on a total of 119.8 hours of exposure of six potometers in each of three stations while the atmometer records are for a total of 76 days.

CONCLUSIONS

The pines showed a greater rate of diameter increase than the other species considered. They also transpired more per gram of green leaf per hour throughout the season. Young ponderosa pines and lodgepole pines of initial stands had a faster rate of growth than the Douglas fir. We can thus conclude that the pines have a greater rate of diameter increase, a faster rate of growth, and transpire more than the Douglas fir. Since the sub-alpine fir and Engelmann spruce approach most closely the rate of growth of the Douglas fir and since the least water was given off in their habitat, we can place it in the same comparative rank with the Douglas fir.

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SUMMARY

This study is based on data secured from conifers growing within and near Rocky Mountain National Park.

The five species considered are: *Pinus contorta*, *P. ponderosa*, *Pseudotsuga taxifolia*, *Picea Engelmannii*, and *Abies lasiocarpa*.

Four stations were established; one in the lodgepole, one in the ponderosa pine, one in the Douglas fir, and one in the Engelmann spruce area. The most intensive studies were carried out in the first three stations.

Measurements on the rates of diameter increase were obtained from increment cores taken from the north and south sides of about 1000 trees. Height growth rates were determined by examining seedlings and saplings and from older lodgepole pines.

The type of forests formed by the lodgepole pine, the ponderosa pine, and the Douglas fir is shown by a study of the crown mosaics of these species. The distribution of the woody undergrowth is also recorded in these crown projection maps. Herbaceous plants are recorded for the mapped portion of these three stations.

The average diameter (D.B.H.) increase per year based on all measurements made for the various species was: lodgepole pine 1.77 mm., ponderosa pine 1.54 mm., Douglas fir 1.53 mm., sub-alpine fir 1.35 mm., and Engelmann spruce 1.30 mm. The increase per year for all trees during the century 1833 to 1932 was ponderosa pine 1.83 mm., lodgepole pine 1.81 mm., sub-alpine fir 1.54 mm., Engelmann spruce 1.41 mm., and Douglas fir 1.37 mm.

Water loss from atmometers ranked in the same order as water transpired from cut shoots. The ponderosa pine environment showed the greatest loss, the Douglas fir areas ranked second, the lodgepole pine third, and the lowest water loss was in the area of the Engelmann spruce.

According to potometer data, the lodgepole pine transpired the most, the ponderosa pine ranked second, and the Douglas fir transpired the least. These responses were modified according to the station environment indicated above.

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1931–1935

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